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BIRDS OF THE ISLE OF PINES.

OUTRAM BANGS AND W. R. ZAPPEY.

INTRODUCTION.

THE following account of the birds of the Isle of Pines is, for the most part, based on a large collection and field notes made by one of us (Zappey) in the spring and early summer of 1904. Zappey had, however, visited the island once before — in March, 1902 — and the few birds, mostly North American migrants, taken on that trip that were not observed on the later one, are included.¹ In addition to this material, William Palmier and J. H. Riley, who spent two weeks in July, 1900, near Nueva Gerona, have most kindly placed in our hands their notes and lists of birds observed and taken. And lastly, in order to make our list complete, we include such species as were recorded from the island by Poey, by Cory, and by Gundlach.

Mr. Riley has made many comparisons for us with the material in the United States National Museum, and has otherwise done everything in his power to help us, and we here express our most hearty thanks for all his kindness.

¹ This first collection, unfortunately, did not remain in this country but went to the Tring Museum, and thus far has not been reported upon.

LITERATURE.

While no very complete list of the birds of the Isle of Pines has been published, many references to the ornithology of the island can be found in the writings of Poey, Cory, and Gundlach,

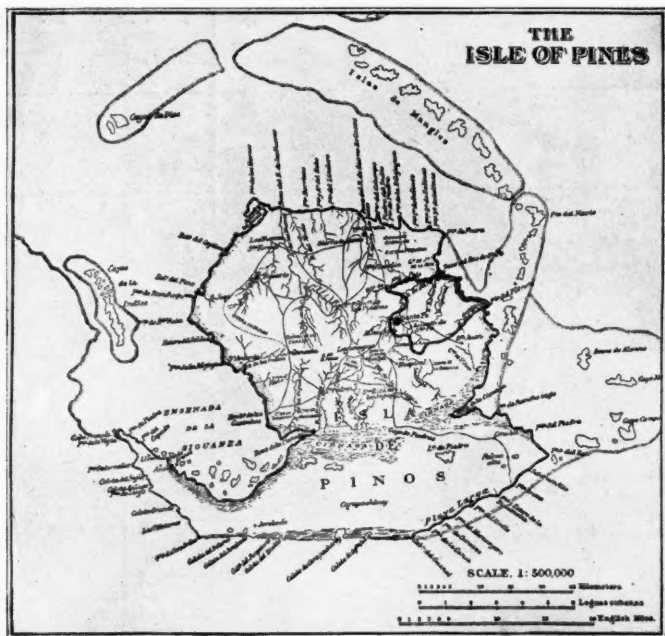


FIG. 1.—Map of the Isle of Pines.

and in the three parts that have already been issued of Ridgway's *Birds of North and Middle America*. The full references to these works are as follows:—

Felipe Poey, *Memorias sobre la Historia Natural de la Isla de Cuba*, 1854.

(Tomo 1, pp. 426-427; a nominal list of birds observed by Gundlach during a six days' stay at Nueva Gerona.)

C. B. Cory, *Catalogue of West Indian Birds*, 1892.

(Numerous references to the birds of the Isle of Pines, probably from MSS. furnished the author by Gundlach. The Isle of Pines appears in the distribution of the various species, usually as Greater Antilles, No. 2.)

Juan Gundlach, *Ornithologia Cubana*, 1895.

(The last work of this distinguished Cuban ornithologist, containing many references to the birds of the Isle of Pines.)

Robert Ridgway, *The Birds of North and Middle America*. Bulletin of the United States National Museum, No. 50. Part I, 1901; Part II, 1902; Part III, 1904.

(Each species known to the author to occur on the Isle of Pines, is recorded from there, and in one or two instances measurements are given for comparison and critical remarks made, as for example in the case of the Spindalis.)

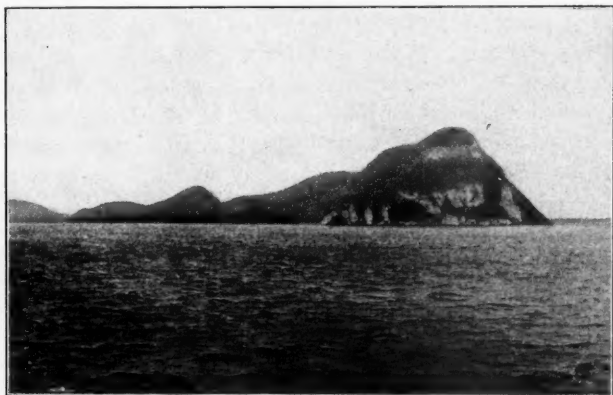


FIG. 2.— Isle of Pines, as seen from the northeast. The rocky islet in the foreground was the roosting place of hundreds of Cormorants and a few White Ibises.

PHYSICAL ASPECT OF THE ISLE OF PINES AND CLIMATE.

The Isle of Pines lies about 60 miles south of Cuba, and can be reached by rail from Havana to Batabano and thence by sailing vessel or steamer to the island.

The Isle of Pines is about 30 by 40 miles in extent, containing some 1240 square miles, or a trifle less than the State of Rhode Island. It is divided into two parts, the northern one

being the larger, by a fresh-water swamp, the "Cienaga," that runs across the island from east to west.

The land south of the Cienaga is of coral formation with a very shallow soil spread over the coral rock, and with deep holes or pits everywhere. A number of prints of fossil shells of various kinds were observed in the coral rock. Fires devastate this part of the island, burning up the soil and the very roots of the trees and leaving nothing behind but the bare coral rock, and the region is very sparsely inhabited. The trees of this region are mostly hard wood, there being no pine and very few royal palms.

North of the Cienaga, the country is of a very different char-

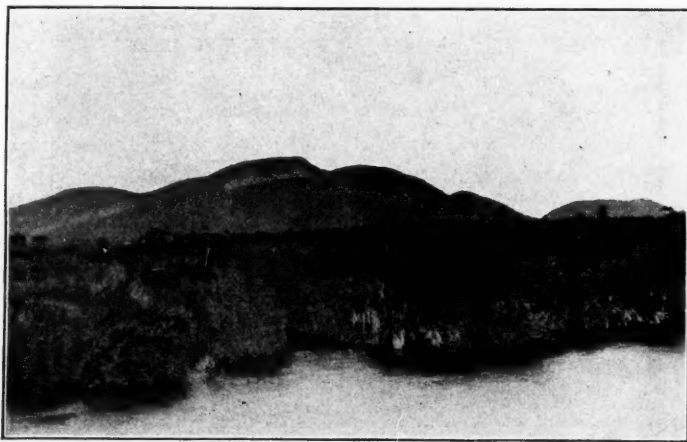


FIG. 3.—Casas River, Caballos Mountains in the distance. Mangrove bushes in the foreground along the river, and as the land rises, dense palmetto scrub.

acter. There are here a number of mountains rising abruptly from the plain, Pico de la Dacuilla, the highest, having an altitude of about 2000 feet. The flat country is diversified by pastures, cultivated fields, open pine woods, and groves of royal palms and palmettos and along the water courses there are dense tropical forests. The mountain sides are very rocky and are clothed chiefly with scrub and thorn bushes and, where there is soil enough, some good-sized trees. The banks of the rivers and

many parts of the shore of the island are fringed with mangroves which give way as the land rises, to a dense growth of palmetto.

In the Isle of Pines the rainy season begins in the early part of May, and rain falls continually until October. The character of the country is entirely changed. The Cienaga is covered by two or three feet of water and the rivers, which are nearly dry in the dry season, become torrents.

Great difficulty was experienced in taking photographs especially after the rain began, but the accompanying views selected from a great many, give some idea of the general character of the island.

BIRDS.*

About eighty-three species of birds, most of them resident, breed in the Isle of Pines.¹ Besides these, a few northern species either winter there or make a short stop in spring or autumn, but the list of migrants thus far is not a long one.

Owing to its nearness to Cuba and to the fact that, geologically speaking, its separation from that island was recent, one would not look for any marked peculiarities in the birds of the Isle of Pines, and such do not exist. Nevertheless many of the birds of the island have already become slightly changed and although they strictly represent the Cuban species, it seems best to give some of them distinctive names. The changes that have thus far taken place are chiefly in size and proportions, colors in most of the species remaining the same or very similar. There is no rule in these changes in size,—some of the birds of the Isle of Pines are larger, others are smaller than their Cuban representatives.

All the birds of the island are well known by the natives, who have a name for nearly every species. In the following list we give these names. In some cases we may be slightly in error in the spelling of them as it is impossible to find a native who can write them correctly.

¹ This number includes some species probably now extinct and a few larger birds—such as the Frigate Bird and Flamingo—that may or may not actually breed in the island.

Some species that were seen and not taken by either Zappey or Palmer and Riley, but were probably correctly identified, we give with a question mark. It would be a pity to leave these out of a list of the birds of the island and yet there must ever be a doubt about such records, and this seems to us the best way to treat such cases. A few species, also included in the following list, rest solely on Poey's authority (based on a list furnished him by Gundlach).

Following is a list of the birds¹ of the Isle of Pines, with



FIG. 4.—Country back of the town of Nueva Gerona. Casas Mountains in the distance.

notes on their habits, distribution, etc., and with critical remarks, and descriptions of a few new forms, drawn from the various sources enumerated above.

1. *Podilymbus podiceps* (Linn.).—An adult female and three downy young were found by Palmer and Riley in a small lake near Nueva Gerona. One of the young was taken but the old bird was very wary and could not be secured.

¹The systematic sequence of this list is about the same as that followed by Ridgway in the *Birds of North and Middle America*, now appearing in parts, based principally upon Hans Gadow's *A Classification of Vertebrata, Recent and Extinct*, 1898, only turned about so as to bring the "lower" (less specialized) orders first. Colors are according to Ridgway's *Nomenclature*, and measurements are in millimeters.

Two were shot by Zappey, and one of them saved, in March, 1902, at Laguna Grande, but in the spring of 1904 no Pied-billed Grebes were observed anywhere in the island.

2. *Phalacrocorax dilophus floridanus* (Aud.). "CORNA"
— Cormorants were common along the seacoasts of the island and among the outlying cays, and undoubtedly all birds inhabiting the salt water belong to this form, which has been recorded from Isle of Pines by Cory and by Gundlach. Specimens of the Florida Cormorant were secured by Palmer and Riley on the Cuban coasts, and many were observed at Batabano opposite the Isle of Pines.

3. *Phalacrocorax vigua mexicana* (Brandt). "CORNA."
— One young adult female, was taken in the Cienaga at Pasadita in May. This was the only one observed.

This specimen is rather larger than usual for *mexicana*, but E. W. Nelson who has compared it for us with the large series collected by himself in Mexico, says that it is equalled and even exceeded by some Mexican individuals, and authors generally have considered the Cuban Fresh-water Cormorant to belong to this race rather than true *vigua*.

The skin, no. 13,236, measures: wing, 268; tail, 164; tarsus, 50; exposed culmen, 50.

4. *Anhinga anhinga* (Linn.). "CORNA REAL." — The Anhinga was found by Zappey in the Cienaga only, where it was fairly common and a number might be seen any day sitting on dead branches of trees in different parts of the swamp, with wings and tail extended to the rays of the sun. One was seen by Palmer and Riley at Nueva Gerona.

Two specimens — a fine pair of adults — taken by Zappey, May 28, 1904, do not differ in any way from Florida birds.

5. *Fregata aquila* Linn. "RABIHORCADO." — Occurs occasionally off the south coast of the island, and during a severe storm was seen high in air passing over the town of Santa Fé. Palmer and Riley also saw it at Managua.

6. *Pelecanus fuscus* Linn. "ALCATRAZ." — A few individuals were seen on the south, but none on the north coast.

7. *Pelecanus erythrorhynchos* Gmel. — The White Pelican has been recorded by Cory from Isle of Pines. None were

observed by Palmer and Riley nor by Zappey on either trip. It is probably a very irregular winter visitor to the island.

8. *Ardea repens* sp. nov.

Type from the Cienaga, Isle of Pines, adult ♀, no. 13,241, Coll. of E. A. and O. Bangs. Collected May 24, 1904, by W. R. Zappey.

Characters.—Similar to *Ardea occidentalis* Aud. of south Florida but very much smaller.

Color.—Entirely pure white; the bill yellow; legs and feet greenish yellow.

Measurements.—Type: wing, 440; tail, 156; tarsus, 172; exposed culmen, 144.

Since the ornithology of Cuba has first been known, up to the present time, references to *Ardea occidentalis* can be found in the literature, but specimens do not appear to have been taken. Birds from Cuba and the Isle of Pines are in all probability the same, and certainly cannot be referred to *A. occidentalis*, being far too small. This is all that can be said at present. Future research may prove this bird to be the white phase of the Great Blue Heron of Cuba, but here again there appear to be no specimens, and it is not known to what form that bird belongs. Under the circumstances we have thought it best to give the white bird a name as it certainly is not *A. occidentalis*.

Zappey saw this bird but once—the one taken. Palmer and Riley observed a few about the cays.

9. *Ardea herodias* Linn. (*sub. sp. ?*).—The Great Blue Heron was seen on several occasions in the Cienaga, but was very shy and none were secured. A few were also seen by Palmer and Riley about the cays.

As stated under the preceding species, it is still unknown to what form the Great Blue Heron of Cuba and the Isle of Pines belongs, and possibly it may be the colored phase of the bird we describe as *Ardea repens*.

10. *Herodias egretta* (Wilson). "GARCILATE."—A few Egrets were seen, in different parts of the island, both inland and on the seacoast, always singly, and they were very shy.

In former years it was abundant, but has been nearly extirpated for its plumes.

A fine adult female was taken at La Vega, May 22, 1904, and one was obtained by Palmer and Riley at Nueva Gerona.

11. *Florida cærulea cærulescens* (Latham). "GARGA AZUL." — Very common, being found both on the seacoasts and in the Cienaga.

Two specimens, ♂ and ♀, were taken respectively at Guanawana, May 15, and in the Cienaga, May 23.

12. *Leucophoyx candidissima* (Gmel.). "GARGA BLANCA."



FIG. 5.— Palmetto and royal palms near the Casas Mountains.

— The Snowy Heron is now very rare in the Isle of Pines, having been killed off for its plumes. One was seen in the Cienaga, and at Jucaro a native had a wounded bird that was kept alive in confinement.

13. *Hydranassa tricolor ruficollis* (Gosse). "GARGA." — This species is not uncommon in the seacoast lagoons and the brackish water of the rivers, but was only once seen in the Cienaga.

One female was taken in the Cienaga, May 23, 1904.

14. *Nyctanassa violacea* (Linn.). "GUANABA."—Recorded from Isle of Pines by Poey, Cory, and Gundlach. None were seen by Zappey nor by Palmer and Riley.

15. *Nycticorax nycticorax nævius* (Bodd.).—In March, 1902, a flock of Black-crowned Night Herons was seen at a fresh-water lagoon in the northern part of the island and two others in a salt lagoon at Bibeyhagua. It is also recorded from the island by Poey.

16. *Butorides virescens maculata* (Bodd.). "AQUAITA."—The Green Heron occurs, in small numbers, wherever there is fresh water, and was also occasionally seen along the sea-coast.

As has been pointed out by Riley, all West Indian Green Herons are much alike, and must be called by Boddart's name. The form differs from true *virescens* of the mainland chiefly in being smaller.

Two males were taken: one at Bibeyhagua, May 15, the other at Santa Fé, April 20.

17. *Butorides brunnescens* (Lembeye).—Two specimens of this dark-colored bird were taken by Palmer and Riley near Nueva Gerona.

We cannot avoid a strong impression, despite its peculiar coloration and the fact that young individuals are as different as adults from *B. virescens maculata*, that this supposed species is a color phase of the ordinary bird. This, however, can be proved by careful observation only, by ascertaining whether the two breed together or mate each with its own kind only.

18. *Ardetta exilis* (Gmel.).—The Least Bittern was abundant in the Cienaga in March, 1902. On the 1904 trip, made later in the spring, none were found anywhere, leading to the conclusion that those seen in March were winter residents and that the bird does not breed in the Isle of Pines.

19. *Botaurus lentiginosus* (Montag.).—Recorded by Cory and Gundlach from the Isle of Pines, but not observed by Zappey nor by Palmer and Riley.

20. *Eudocimus albus* (Linn.). "Coco."—One of the commonest and most characteristic birds of the Cienaga, flocks

of from forty to fifty being often seen. It also occurs though not in such large numbers in most parts of the island. It feeds on snails, frogs, and lizards. The natives often tame the White Ibis and it then runs about with the domestic fowl and eats table scraps and the like, which it always carries to the nearest water and soaks before swallowing. These tame birds were also very fond of the bodies of small birds that had been skinned, and would catch them when thrown to them, before they touched the ground.

One specimen was taken, a male, at Pasadita, May 8.

21. *Ajaia ajaia* (Linn.). "CERVEIA."—The natives claim that a few Roseate Spoonbills still occur in the Isle of Pines. The species is recorded by Poey and formerly was not uncommon. It was not seen by Zappey nor by Palmer and Riley.

22. *Tantalus loculator* Linn.—Recorded from the Isle of Pines by Cory. Its occurrence there is probably only casual as it was not found by Zappey nor by Palmer and Riley.

23. *Phœnicopterus ruber* Linn. "FLAMENCO."—A few Flamingoes inhabit Punta del Este and Bibeyhagua. None were seen alive, but one morning the tracks of about a dozen were found in the mud, and on another occasion three individuals that had just been shot by a native were examined.

24. *Chen hyperborea nivalis* (Forst.).—An occasional winter visitor, recorded from the island by Cory and by Gundlach.

25. *Dendrocygna arborea* (Linn.). "LLAGWASA."—The Whistling Duck occurs in considerable numbers in the Isle of Pines. During the day it keeps concealed in the Cienaga but in the evening, toward dusk, it leaves the swamp to feed in the royal palms, alighting on the trees and picking off the berries. One night a half a dozen or so alighted in the palms in the plaza at Santa Fé. The call note of this bird is much like that of the Wood Duck (*Aix sponsa*).

Six specimens, adults of both sexes, were taken in the Cienaga in May.

26. *Querquedula discors* (Linn.).—In March, 1902, the Blue-winged Teal was in the Cienaga in considerable numbers. On the second trip none were found, the species probably leaving for the north before the middle of April.

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27. *Cathartes aura aura* (Linn.). "AURA."—The Turkey Buzzard is very common everywhere in the island. The bird of the Isle of Pines, and other West Indian Islands, is very much smaller than that occurring in the southern United States and



FIG. 6.—Palmetto growth bordering the pine lands. The highest tree in the center of the picture, is a species of pine that grows chiefly near the seacoast north of the Cienaga.

as Wied named the latter *septentrionalis*, Linné's name should be restricted to the small southern form, since he gave the distribution of his *Vultur aura* as North America, Jamaica, Mexico, etc. The Turkey Buzzard of the southern United States should be known as *Cathartes aura septentrionalis* (Wied).¹

¹ *Cathartes septentrionalis* Wied, *Journ. f. Orn.*, p. 119, 1856.

Two specimens, ♂ and ♀, were taken at Santa Fé and measure as follows:—

No.	Sex.	Wing.	Tail.	Tarsus.	Culmen.
13376	♀	483	236	69	38
13377	♂	456	228	69	41

28. *Polyborus cheriway* (Jacq.). "CARAIRA."—This is not a common bird in the Isle of Pines and is extremely shy. Whenever there happens to be a dead animal anywhere, however, one or two Caracaras will always be found near by. They also feed on lizards and are said by the natives to kill small chickens.

One male was taken at Santa Fé, May 20. This specimen does not differ from skins from Florida and elsewhere on the continent.

29. *Urubitinga anthracina* (Licht.). "BATISTA."—The Cuban Crab-hawk is recorded from the Isle of Pines by Poey, as *Hypomorphus gundlachi* Cab.

There are no specimens available to us for comparison of the Cuban bird, and we are therefore forced to follow the general custom of placing it under true *U. anthracina*.

The species was not detected in the island by Zappey nor by Palmer and Riley.

30. *Rostrhamus sociabilis* (Vieill.). "CARBRETO."—Common in the Cienaga and also seen at Santa Rosalia lagoon. Its food consists of small snails, though the natives assert that it eats frogs and lizards also.

One male taken at the Cienaga, May 23, is in every way like specimens from Florida.

31. *Falco peregrinus anatum* (Bonap.). "HALCÓN."—One was examined in March, 1902, that had struck and killed a hen, and being either unable or unwilling to let go, was chopped to pieces by some natives with their machetes.

32. *Falco columbarius columbarius* Linn.—Recorded from the Isle of Pines by Cory and by Gundlach as an occasional winter visitor.

33. *Cerchneis sparveria dominicensis* (Gmel.). "CERNICALO."—Very common everywhere in the island. This form has the same habit as the Sparrow Hawk of Florida, of congre-

gating in numbers wherever the brush or grass has been set on fire and hovering just in front of the flames. In the Isle of Pines they appear to get small lizards only in this way, there being no small mammals.

Seven specimens were taken at Santa Fé, San Juan, Jucaro, Laguna Grande, and Almacigos, in April and May. Of the great number seen, one only was in the dark phase of plumage, and Palmer and Riley state that *all* observed by them were in the white-bellied plumage.

34. *Pandion haliaetus carolinensis* (Gmel.).—Recorded from the Isle of Pines by Cory; not observed by Zappey nor by Palmer and Riley.

35. *Colinus cubanensis* (Gould). "CODORUIZ."—The Cuban Quail was common in the pastures and fields about Santa Fé and Nueva Gerona, where they were nesting in May.

Three males were taken at Santa Fé and Callebón in May; these specimens do not differ in any way from Cuban examples.¹

36. ? *Rallus elegans* Aud. "GALLINUELA."—In March, 1902, a large rail was rather common in the Cienaga, and several specimens were taken. None could be found on the later trip and the bird apparently does not breed in the island. (The skins taken on the first trip are in the Tring Museum, but Zappey is sure they were referable to the King Rail.)

37. *Gallinula galeata* Bonap. "GALLINETA."—In March, 1902, a few individuals were found in Santa Rosalia lagoon. None were met with on the later trip and it is probable that the gallinule does not breed in the island. Recorded from the Isle of Pines by Cory.

38. *Ionornis martinica* (Linn.). "GALLINUELA."—The Purple Gallinule breeds abundantly in the Cienaga but was not noted anywhere else in the island.

Four males were taken in the Cienaga at Pasadita, in May and June. These specimens are slightly larger than examples from the mainland of the southern United States, measuring as follows:—

¹ The Guinea Fowl (*Numida meleagris* Linn.), and the Domestic Hen (*Gallus* sp.?), have both run wild in the Isle of Pines, and are occasionally found throughout the island, apparently perfectly naturalized.

No.	Sex.	Wing.	Tail.	Tarsus.	Bill. ¹
13,232	♂ ad.	182	70	59	31
13,233	♂ ad.	183	79.5	63.5	30
13,234	♂ ad.	190	75	59	30.5
13,235	♂ ad.	179	69	61.5	31

39. *Fulica americana* Gmel.—Recorded from Isle of Pines by Cory and by Gundlach. Not noted by Zappey nor by Palmer and Riley. As with many other species that are winter residents in the Isle of Pines, the trips made by Zappey and by Palmer and Riley were too late in the season to find these birds still in the island.

40. *Grus nesiotes* sp. nov.²

“GRULLA.”

Type from La Vega, Isle of Pines, adult ♂, no. 13,238, Coll. of E. A. and O. Bangs. Collected May 8, 1904, by W. R. Zappey.

Characters.—Similar to the Sandhill Crane of Florida, (usually called *Grus mexicana* Müll.) in color, but slightly darker and not so clear a gray on back; smaller with shorter tarsus; beak somewhat stouter and heavier.

Measurements.³—

No.	Sex.	Locality.	Wing.	Tail.	Tarsus.	Culmen.
13,238	♂ ad.	Isle of Pines, La Vega	474	187	209	125
13,239	♂ ad.	Isle of Pines, Pasadita	460	171	204	123

¹ Measured from a point in line with eye and nostril to tip.

² This bird may or may not be considered different enough from the Sandhill Crane of North America to rank as a full species; we have given it a binomial because we fully agree with Dr. Sharpe that the bird called *Ardea (Grus) mexicana* by P. L. S. Müller is not the one to which the name is generally applied—the Sandhill Crane of North America. Until the synonymy of these birds is properly adjusted it is better not to give the Isle of Pines Crane as a subspecies.

³ For comparison with these, specimens from the United States measure as follows:—

No.	Sex.	Locality.	Wing.	Tail.	Tarsus.	Culmen.
684	♂ ad.	Wisconsin	508	202	230	135
691	♂ young.	N. Dak., Harrisburg	518	187	224	124
10,717	♂ ad.	Fla., Micco	514	192	238	125
10,718	♂ ad.	“ “	494	195	248	132
4107	♂ ad.	Fla., Henderson Camp	470	170	223	128
4106	♀ ad.	“ “ “	444	159	217	122
10,716	♀ ad.	Fla., Haines City	465	188	247	136

The Sandhill Crane is rare and of local distribution in the Isle of Pines, and was only met with in the high, open country just north of the Cienaga, where it usually occurred in pairs, though on one occasion a flock of six was seen. When disturbed, it utters a loud honking or gobbling call note not unlike some of the sounds produced by the Domestic Turkey. The birds seen were always exceedingly shy, and the two specimens were secured with a good deal of difficulty.

On May 20, a small downy young individual was found running about alone. It was exactly the color of the soil. It was kept alive for a day or two but would not eat anything given it. The skin is that of a young not long hatched. It is covered with down which is tawny along the back, tawny-ochraceous on sides, and whitish on throat and middle of belly.

After careful comparison of a large series of North American Sandhill Cranes, we feel fairly sure that the birds still breeding in Florida are not different from those that breed in North Dakota and other parts of the west. Probably in former years the breeding range was continuous or nearly so, and it is due to the interference of man that the Florida bird is now isolated.

In the breeding season the Sandhill Crane is much browner, — losing most of the pearly gray of the back and neck, — than in fresh autumn plumage, and this is true of birds both from the west and from Florida. Unfortunately, however, we have seen *only* breeding birds and birds killed in early spring from Florida, and therefore no gray ones, but we have no doubt that fresh autumnal specimens from Florida would be quite as gray as those from the west. In measurements there is no difference.

The bird of the Isle of Pines, and almost certainly Cuba also, differs from that of the continent in its decidedly shorter tarsus, heavier bill, and slightly smaller size. In color the difference is slight, but still our two Isle of Pines skins are rather darker and browner than any breeding Florida birds with which we have been able to compare them.

41. *Aramus giganteus holostictus* (Cab.).¹ "GUARACAO."

¹ *Nothrodicus holostictus* Cabanis, *Journ. f. Orn.*, p. 426, 1856, based on Cuban specimens.

—The Limpkin was found in the Cienaga only, where it was far from common, and where one adult male was taken in May.

This specimen is smaller, with shorter tarsus, and much shorter and smaller bill, than any in a large series of Florida birds with which we have compared it. It is also paler in general coloration; the tail is lustrous olive brown (dark, lustrous purple in true *A. giganteus*) and the white markings on wings, wing-coverts and scapulars are smaller. The skin, no. 13,237, ♂ ad., measures: wing, 308; tail, 138; tarsus, 114; exposed culmen, 110.

We have therefore thought it best to recognize the Cuban and Isle of Pines birds as a subspecies.

42. ? *Ochthodromus wilsonius rufinucha* (Ridg.). "FRILECILLO." — A few birds, undoubtedly belonging to this form, were seen along the shore at Plaza Larga, but none were secured.

43. *Oxyechus vociferus torquatus* (Linn.).¹ "FRILECILLO." — A few pairs of Killdeer breed in the Isle of Pines. They were seen on several occasions, and a young in the down was caught, but let go again at the beach at Bibeyhagua.

One adult male was taken April 21, at Laguna Grande, and Palmer and Riley took specimens at Nueva Gerona.

The breeding Killdeer of the Greater Antilles is a good deal smaller than the bird of continental North America and should be recognized as a subspecies.

Our specimen, ♂ ad., no. 13,335, measures: wing, 146; tail, 82.5; tarsus, 34; exposed culmen, 21.

The larger Killdeer of the north winters in many of the islands, and this fact must be borne in mind in identifying specimens, else confusion is sure to ensue. There is no trouble in distinguishing the two forms, however, when breeding birds are compared.

44. *Himantopus mexicanus* (Müll.). "ZARAPICO REAL." — Two Black-necked Stilts, one of which, an adult female, was taken, were found in the Salina at Bibeyhagua, May 15. The

¹ *Charadrius torquatus* Linn., *Syst. Nat.*, vol. 1, p. 255, 1766, based on *Pluvialis dominicensis torquata* Briss., *Aves*, vol. 5, p. 70, pl. VI, fig. 2, from Santo Domingo.

species is probably of very casual occurrence anywhere in the West Indies.

45. *Catoptrophorus*¹ *semipalmata semipalmata* (Gmel.). "ZARAPICO REÁL."—No Willets were met with by Zappey nor by Palmer and Riley. It is recorded from the Isle of Pines by Poey.

46. *Totanus melanoleucus* (Gmel.). "ZARAPICO REÁL."—One specimen, an adult female, was taken at the Salina at Bibeyhagua, May 15.

47. *Totanus flavipes* (Gmel.).—In March, 1902, specimens of the Summer Yellowlegs were taken, but none were observed on the last trip to the island.

48. *Helodromas solitarius solitarius* (Wils.). "ZARAPICO."—One adult female was taken May 11, at Jucaro; it was in a little puddle at the roadside left by a heavy shower.

49. *Actitis macularia* (Linn.).—Spotted Sandpipers were not uncommon about the shores of the island in March, 1902. None were seen on the last trip.

50. *Asarcia spinosa* (Linn.). "GALLITO."—The Jaçana occurs in every fresh-water lagoon, but is most abundant in Santa Rosalia lagoon and the Cienaga.

When disturbed it stretches up its wings and runs along over the lily-pads and weeds for a short distance before taking flight, at the same time uttering a loud alarm note that sets all others in the vicinity to flying.

Three specimens were taken at Laguna Grande and Pasadita, in April and May.

51. *Sterna maxima* Bodd. "GAVIOTA."—The Royal Tern was common along the seacoasts of the island and on the mangrove cays. Several were shot, but fell into the ocean and before they could be retrieved, were gobbled up by sharks.

52. *Columba inornata* Vig. "PALONEA BABO," "TORCAZA."—One specimen of this pigeon was taken in March, 1902. It was not met with at all on the second trip and is said by the natives to be very rare in the Isle of Pines. It is among the species given from the island by Poey.

¹ Cf. Richmond, *Proc. Biol. Soc. Washington*, vol. 18, p. 75, Feb. 21, 1905.

53. *Columba leucocephala* Linn. "TORCAZA CABEZA-BLANCA."—The White-crowned Pigeon is not uncommon along the river courses, especially where there are royal palms, upon the fruit of which it feeds.

Two specimens, both males, were taken at La Vega in April.

54. *Columba squamosa* Bonn.—Palmer and Riley inform us that this species occurs in the vicinity of Nueva Gerona but is rare there.

55. *Zenaidura macroura bella* Palmer and Riley. "PALOMA."—Throughout the island in the open pine woods, palmetto groves, and especially in old fields grown up to weeds, the Cuban Mourning Dove is an abundant bird. Several nests were found in low trees five or six feet from the ground.

Three specimens, two males and a female, were taken at Rio Santiago and Hospital in May. These are similar in every way to Cuban examples.

56. *Zenaida zenaida zenaida* (Bonap.). "PALOMA."—The Zenaida Dove inhabits the same sort of country as the last species, the two being found together, but it is not so abundant.

Two specimens, both males, were taken at Almacigos, April 19.

57. *Columbigallina passerina aflavida* Palmer and Riley. "TOJOSITA."—Common everywhere in the island except in the denser woods. Several nests were found placed on the ground, containing two eggs each.

Seven specimens, of both sexes, were secured at Callebónita, Hospital, Jucaro, and San Juan, in May. These do not differ at all from Cuban specimens.

58. *Geotrygon montana* (Linn.). "BOYERO."—The Ruddy Quail-dove occurs in the Isle of Pines in the denser woods only, usually in rather moist places, where the ground is often flooded after heavy rains. It is nowhere abundant. When flushed from the ground it flies but a short distance and on alighting again runs along for a few feet and conceals itself among the vegetation much after the manner of the American Woodcock (*Philohela minor*), which it curiously resembles when started in the deep woods.

Six specimens, including both sexes, were taken at La Vega, Pasadita, and Callebonita in May and June.

These skins are not to be distinguished in any way from skins from Jamaica, the type locality of the species.

59. *Geotrygon chrysia* (Bonap.). "CANÍAO."—The Key

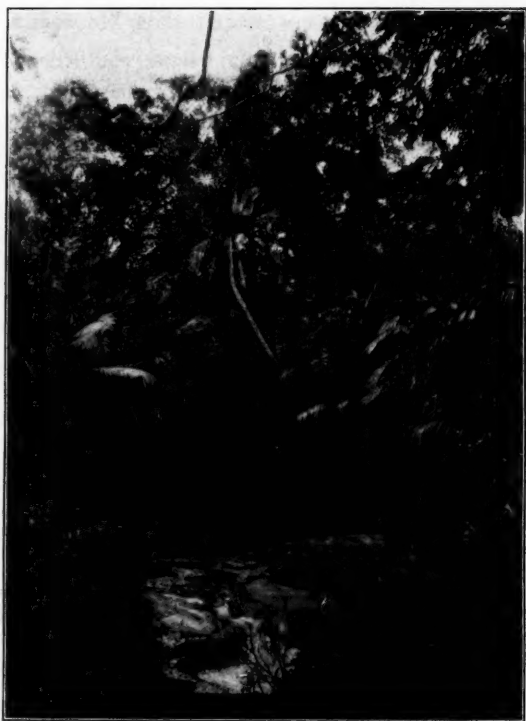


FIG. 7.—Callebonita River before the rainy season when the water was very low. "Guana blanco" palms in the foreground.

West Quail-dove is very rare in the Isle of Pines occurring only on one or two of the mountains and in the dense forest south of the Cienaga.

Only two individuals were seen. These were both secured, at Pasadita, one in May the other in June.

60. *Starnoenas cyanocephala* (Linn.). "PERDIZ."—This bird has not been actually seen by any naturalist in the Isle of Pines. We include it because the natives who know it well positively assert that a few inhabit the Caballos Mountains and some point near the south coast.

61. *Saurothera merlini decolor* subsp. nov.

"ARRIERO."

Type from La Vega, Isle of Pines, adult ♂, no. 13,246, Coll. of E. A. and O. Bangs. Collected April 24, 1904, by W. R. Zappey.

Characters.—Somewhat similar to true *S. merlini* d'Orb. of Cuba, but smaller, with decidedly shorter bill; much paler in color, wholly lacking the hazel or pale chestnut suffusion of back, head, and rump, these parts being, in the new form, uniform dull hair-brown; the ferruginous color of the lower underparts also much paler and duller and more restricted, never reaching the lower breast. In general coloration the Isle of Pines bird—except for the chestnut patch in the wing—more nearly resembles *S. bahamensis* than *S. merlini merlini*.

The young is like the adult except that it lacks the black sub-terminal band to the rectrices.

Iris brown, bare skin around eye scarlet, legs slate blue (from fresh specimen just killed).

Measurements:—

No.	Sex.	Wing.	Tail.	Tarsus.	Culmen.
13,246	♂ ad.	163	267	42.5	52.5
13,247	♂ ad.	161	262	43	55
13,243	♂ ad.	164	235	43	52
13,242	♂ ad.	158	255	41.5	51.5
13,244	♀ ad.	149	226	39.5	50
13,245	♀ ad.	161	252	40.5	54

The Lizard Cuckoo of the Isle of Pines is a common bird in rough, rocky country wherever there is a thick growth of scrub and bushes, and is very tame. It has a habit of hopping from one branch to another till it reaches the top of a bush and then sailing down to the ground or the lower branches of another

bush. Its usual call note is a sort of laugh that begins low and slowly, and rapidly ascending, ends in a loud chuckle. When two individuals are within sight of each other they often go through a curious performance, which consists in lowering the head and dropping the feathers of the throat which then looks like a large pouch, at the same time spreading the wings and tail to their fullest extent and repeating the loud chuckling notes that end the usual call. The stomachs of those taken contained the remains of small lizards, beetles, caterpillars, and large moths.

Seven specimens were taken, adults of both sexes and one young, at La Vega, Callebón, and Hospital, in April, May, and June.

The Isle of Pines *Saurothera* is a very well marked form differing much from true *S. merlini* of Cuba in size and proportions as well as in its paler and plainer coloration, and perhaps should be considered a distinct species. We, however, prefer to treat representative island forms as subspecies, unless they present even more strongly marked characters than do these two cuckoos. By so doing, the affinities of a bird are seen at a glance by its name, whereas, by the use of binomials they are lost.

62. *Crotophaga ani* Linn. "JUDIO." — The Ani is a common bird in the Isle of Pines, occurring in all pastures, in brushy regions, and along the river courses. It was often seen on the backs of horses, cattle, and hogs picking off ticks.

Five specimens were taken at Callebón, Santa Fé, and Jucaro, in April and May.

63. *Ara tricolor* (Bechst.). "GUAEMÁYO." — It has been supposed that perhaps the Cuban Macaw still lingered in the Isle of Pines. Unfortunately this is not so. The last pair known in the island was shot at La Vega, near the Cienaga, about the year 1864, and none have been seen since. This information was furnished by the man on whose plantation they were shot.

64. *Conurus euops* (Wagler). "PERQUITO." — Formerly abundant in the Isle of Pines, the paraquet has been nearly if not quite exterminated in very recent years. Nothing was seen of it and the natives all said that none now occur in the island.

65. *Amazona leucocephala* (Linn.). "COTORRA." — The parrot is still common in the central part of the island, but is rare south of the Cienaga — a few pairs only being seen in some royal palms at Pasadita.

In May, the parrots were breeding. The nests usually contained young though several were examined in which there were eggs, four in number, of a whitish color. The nesting site is invariably an old woodpecker's hole in the trunk of a species of palm that has a large swelling about midway up. The parrot feeds largely in the pines, eating the ends of the new shoots that are soft and green.

Hundreds of young birds are taken annually by the natives and sent alive to the United States. The exporting of live parrots being the chief industry of the island, nearly every nest on the island is found and robbed every year, and although the natives do not kill the old birds and dislike very much to have them shot, nevertheless the parrot is steadily decreasing in numbers year by year, and must inevitably go the way of the macaw and the paraquet unless some steps are taken to protect it.

One adult male was taken at Hospital, May 12. This does not appear to differ in any way from Cuban examples.

66. *Todus multicolor* Gould. "PODORERA." — Along the river courses and dry gulches, where there is a thick growth of brush, the little Tody is frequently met with sitting upright on a branch from which it occasionally darts to catch some insect on the wing, its wings as it does so making a loud whirring sound.

Its call note is a curious sound much like that produced by hitting two small stones together.

Eleven specimens, adults of both sexes, were taken at Santa Fé and Callebónita in April and May, and are quite the same as Cuban examples.

67. *Ceryle alcyon* (Linn.). "MARTIN ZAMBULLIDOR." — The Belted Kingfisher is a regular winter visitor to the Isle of Pines. In March, 1902, it was not uncommon, but on the last trip none were seen, all having probably left for the north.

68. *Nyctalops stygius siguapa* (d'Orb.).¹ "SIGUAPA." —

¹ *Otus siguapa* d'Orb., in Ramon de la Sagra's *Histoire de l'Isle de Cuba, Oiseaux*, p. 40, pl. 2, 1839. Based on Cuban specimens.

The Cuban Eared Owl inhabits in the Isle of Pines the heaviest and densest forests only. It is very rare, and being wholly nocturnal is extremely hard to obtain.

One fine adult male was taken at La Vega, May 25. This specimen compared with three continental examples,—one each from Brazil, Mexico, and Guatemala—differs in being less buffy both above and below, the under parts are much whiter, and the facial disk is white. It is probable that the Cuban bird is the same, and the island race named by d'Orbigny seems a perfectly valid one.

69. *Gymnasio lawrencei* (Scl. and Salv.). "COTUNTO."—This queer, long-legged little owl, with much the general appearance of a Burrowing Owl is strictly nocturnal, spending the day in hollow trees. A pair taken at Santa Seville, May 31, had with them a brood of three half-grown young in a hole in a tree. These young birds were kept alive for a time and were then given to a native, who like so many of his countrymen was very fond of taming and keeping birds in confinement.

Three specimens, two adult males and an adult female, were taken at Pasadita and Santa Seville, in May. These skins compared with a series of six from Cuba show a slight difference in color, being paler with less of a brownish or rufous cast than the Cuban specimens. In measurements they do not differ, and the slight color difference may or may not hold in larger series from the two islands.

70. *Glaucidium siju* (d'Orb.). "SIJU."—One of the characteristic bird-sounds of the island, with which one soon becomes very familiar, is the cry of this little owl. Though the bird is diurnal, its call is often heard at night as well as by day. It is generally distributed throughout the island and is very common.

The stomachs of those taken contained nothing but insects, beetles of various kinds forming the greater part of the contents.

Six specimens, adults of both sexes, were taken at Santa Fé and Callebonita in April, May, and June. These are indistinguishable from Cuban specimens.

71. *Strix pratincola furcata* (Temm.). "LECHUZA."—The Barn Owl is not at all common in the Isle of Pines. But two were seen and two others heard at night.

One adult female was taken at Santa Seville. It had been eating a Ruddy Quail-dove (*Geotrygon montana*).

72. *Chordeiles virginianus virginianus* (Gmel.). — Probably an irregular migrant, though it is recorded from Cuba by Cory.

On May 10, a male was flushed from the ground and alighted in a pine, at Santa Fé, where it was shot. This specimen measures: wing, 200; tail, 105; tarsus, 14; culmen, 8. It is in every way like birds that breed in New England.

73. *Chordeiles virginianus minor* (Cab.). "CERICADAY." — Common everywhere in the island in the more open country and among the pines. In rainy weather it was often seen flying during the day, and at other times roosting lengthwise on a pine limb.

Five specimens were taken at Almacigos, Santa Fé, and Hospital, in April and May.

Chordeiles virginianus minor like many other species of birds of somewhat similar general coloration, appears to be dichromatic, having a rusty and a gray phase of plumage, regardless of sex, age, or season. In the present series all are in the rusty phase of plumage except one female that is very gray. In a series from Cuba we find both phases — one male from Holquin, May 31, being quite the color of Florida specimens of *C. virginianus chapmani*. That it is not that form can of course be told by its smaller dimensions.

74. ? *Antrostomus vociferus* (Wilson). — Recorded from the Isle of Pines with a query by Poey. We consider this an extremely doubtful record probably applying to the next species.

75. *Antrostomus cubanensis* Lawr. "GUARAIBA." — A bird of this species was started from the ground in the dense woods south of the Cienaga in June, and was shot, but was so mangled that it could not be saved. It was the only one seen.

76. ? *Hemiprocna zonaris pallidifrons* (Hartert). — Palmer and Riley saw about the crest of the mountain at Nueva Gerona some large swifts, that they felt confident belonged to this form.

77. *Riccordia ricordii* (Gerv.). "ZUNG ZUNG." — The hummingbird is rather generally distributed throughout the island,

though nowhere abundant. Several nests were found containing two eggs each. It is a noisy little bird and its mouse-like, squeaking note is uttered at frequent intervals, especially when anything attracts its attention.

Four specimens, adults of both sexes, were taken at Almacigos and Santa Fé, in April, May, and June.

78. *Prionotelus temnurus vescus* subsp. nov.

"TOCORORO."

Type from Almacigos, Isle of Pines, adult ♂, no. 13,250, Coll. of E. A. and O. Bangs. Collected April 19, 1904, by W. R. Zappey.

Characters. — Similar to true *P. temnurus* (Temm.), of Cuba in color-pattern and probably in color also. (The Isle of Pines series was taken in spring and early summer, and all Cuban specimens with which we have been able to compare them, in winter, except one. The red belly-patch in the Isle of Pines specimens is much paler and more pinkish — less geranium red — than in the Cuban skins, but the one summer specimen from Cuba is like them in this respect and this difference in the color of the belly-patch is probably due to fading). Much smaller with much shorter tail; in the new form the wing averages 114.11, the tail 107.55; in true *P. temnurus* the wing averages, 123.41, the tail 119.41.

Iris bright carmine, lower mandible red (from fresh specimen before skinning).

Measurements: —

No.	Sex.	Wing.	Tail. ¹	Tarsus.	Culmen.
13,250	♂ ad.	113.5	104	18	19.5
13,251	♂ ad.	115	104	18	19
13,254	♂ ad.	114	106	17.5	19.5
13,255	♂ ad.	113	110	18.5	18.5
13,258	♂ ad.	114	108	18.5	18.5
13,252	♀ ad.	115	107	18	19
13,253	♀ ad.	113	108	17.5	18.5
13,256	♀ ad.	115.5	113	17.5	18
13,257	♀ ad.	114	108	17	18.5

¹ In every instance the tail is measured to the end of the longest *shaft*, not the end of the projecting webs.

For comparison with these a series from Cuba measures as follows:—

No.	Sex.	Locality.	Wing.	Tail.	Tarsus.	Culmen.
14,927	♂ ad.	Cuba, Halquin	124	118	19	19
14,928	♂ ad.	" "	123	118	18.5	17.5
14,925	♂ ad.	" "	123.5	120.5	18	18.5
14,926	♀ ad.	" "	121	117	18	18
11,976	♂ ad.	Cuba, El Guama	124	120	18	20
11,975	♀ ad.	Cuba, San Diego de los Baños	125	123	19	18.5

The Trogon is rather common in the dense woods and along



FIG 8.—Ciénaga, at Pasadita, a short time after the rains had begun. (The birds held up are Sandhill Crane and the White Ibis.)

the river courses. It is a stupid sluggish bird and very tame. Its food consists of fruits of various kinds.

Nine specimens, adults of both sexes, were taken at Puebla Nuevo, Almacigos, Pasadita, and Callebonita, in April and May. These are so very much smaller than Cuban examples that we have thought it best to separate the Isle of Pines bird as a sub-

species, though its smaller size seems to be the only character by which it can be distinguished.

79. *Melanerpes superciliaris* (Temm.). "CARPINTERO." — An extremely abundant and very noisy bird, found over nearly all the island.

Eight specimens, adults of both sexes and two young, were taken at San Juan, Jucaro, Nueva Gerona, and Almacigos, in April, May, and June. These skins run slightly smaller than Cuban ones and have less of the olivaceous tinge below and slightly less red on the belly. All of these characters, however, are rather inconstant and the form though slightly different is not enough so to be regarded as a subspecies.

The young — a male and a female taken June 4 — differ from the adults in having the feathers of the breast, belly, and back tipped with dull scarlet; the scarlet of head duller, more orange; the female has scarlet tips to the feathers of the middle of the crown and differs from the male, only in having the frontal band wider and dull gray instead of white.

The skins measure as follows: —

No.	Sex.	Wing.	Tail.	Tarsus.	Culmen.
13,262	♂ ad.	134	90	27.5	37.5
13,261	♂ ad.	140	92	28	40
13,259	♂ ad.	134	91	26	38.5
13,260	♂ ad.	134.5	91.5	26.5	36.5
13,263	♀ ad.	133	95	26	36
13,264	♀ ad.	130	85 much worn	26	35.5

80. *Sphyrapicus varius varius* (Linn.). — A migrant or winter visitor in the Isle of Pines, first recorded by Poey. In March, 1902, several individuals were seen, but none were noted on the last trip, as it was too late in the season.

81. *Xiphidiopicus percussus* (Temm.). "CARPINTERO REAL." — The Green Woodpecker is common in the Isle of Pines and generally distributed, and its low grating croak soon becomes a familiar sound.

Eight specimens, adults of both sexes, were taken at Santa Fé, Callebonita, and Jucaro, in April and May. These are not to be distinguished from Cuban specimens.

82. *Pitangus caudifasciatus* (d'Orb.). "PITIRRE." — A

not uncommon species along the river courses but always found near water. One nest was found in a palmetto close to the trunk about eight feet from the ground.

Nine specimens were taken at Santa Fé, Hospital, Jucaro, and Callebónita River, in April, May, and June.

83. *Blaticus caribæus* (d'Orb.). "BOBITO."—This little flycatcher was found in low trees and among the thinner brush, always near the ground.

Six specimens, adults of both sexes, were taken at San Juan and Santa Fé, in April and May.

84. *Myiarchus sagræ* (Gundl.). "BOBITO."—Common in the pine woods, but not observed elsewhere in the island.

Seven specimens were taken at Santa Fé, Callebónita, and Jucaro, in April, May, and June.

85. *Tyrannus dominicensis dominicensis* (Gmel.). "PITIRRE."—The Gray Kingbird is abundant in the pine woods and scattered palmettos, but avoids the denser forest.

Seven specimens were taken at Santa Fé, Hospital, Callebónita, and Jucaro, in May.

86. *Tyrannus cubensis* Richmond. "PITIRRE DE AGUA."—The huge Cuban Kingbird is rare in the Isle of Pines. Only six were seen, of which five were shot. They were always near water. The natives say that this tyrant-bird catches small fish in the streams after the manner of a kingfisher; the stomachs of those taken, however, contained only remains of insects and a few berries.

Five specimens were taken at Santa Fé, La Vega, Almacigos, and Mal Pais, in May.

None of the Isle of Pines tyrant-birds differ in any way from those of Cuba.

87. *Galeoscoptes carolinensis* (Linn.). "ZORZAL GATO."—A regular migrant or winter resident, often seen during March, 1902, and once observed in April, 1904. Recorded from the island by Poey, Cory, and Gundlach.

88. *Mimus orpheus* (Linn.).—Given as occurring in the Isle of Pines by Cory, the mockingbird is said by the natives to inhabit the south coast in small numbers. None were seen on either trip.

89. *Myadestes elizabeth retrusus* subsp. nov.

"REISENOR."

Type and only specimen from Pasadita, Isle of Pines, adult male, no. 13,435, Coll. of E. A. and O. Bangs. Collected May 25, 1904, by W. R. Zappey.

Characters.—Similar to true *M. elizabeth* (Lembeye) of Cuba in size and proportions, but much paler in color; general color above hair-brown (olive brown in true *M. elizabeth*); ear coverts much paler, wholly lacking the tawny tinge of these parts in true *M. elizabeth*; the ochraceous line running from eye to frontal apex much paler and less conspicuous; eye-ring much paler.

Measurements.—Type, adult male: wing, 88.5; tail, 82; culmen, 12.

The Isle of Pines Solitaire is very rare and occurs in the densest forests only, where, on account of its retiring habits and dull coloration, it is very hard to shoot. Its loud, ringing song can be heard a great distance, and is almost startling in the still forests in which the bird lives. The stomach of the only specimen taken contained a few berries and the remains of insects.

The form can be told at a glance from Cuban specimens on account of its very much paler coloration, and is a strongly marked subspecies.

90. *Mimocichla rubripes rubripes* (Temm.). "ZORZAL."
—A common species, found throughout the island. It keeps rather more to the brush and the woods than does *Merula migratoria*, which it otherwise much resembles in habits. It is a very conspicuous bird as it runs along the ground or hops about in the brush, with wings lowered and tail thrown upward.

Seven specimens, adults of both sexes, were taken at Santa Fé, San Juan, Hospital, and Callebonita in April and May. These seem wholly referable to true *M. rubripes*, differing only in that the rufous tinge of the belly is slightly paler and less extensive.

91. *Polioptila cærulea* (Linn.).—The Blue-gray Gnatcatcher was found in the island in March, 1902, though none were seen

on the last trip. It is also recorded from the Isle of Pines by Poey.

92. *Vireosylva calidris barbatula* (Cab.). "PREDICADOR."—A rather common bird in the Isle of Pines, frequenting trees of medium height. The iris is red-brown.

Ten specimens, adults of both sexes, were taken at Jucaro, Callebónita, and Santa Fé, in April and May.

93. *Vireo gundlachi* Lembeye. "JUAN CHIVI."—Gundlach's Vireo is very rare in the Isle of Pines. One pair was found in some brush and small trees at Callebónita, and secured May 3. These were all that were seen. The natives knew the bird, but said it was an uncommon species.

The two specimens secured differ somewhat from Cuban skins and more material might or might not bear out these differences. If it did, the form from the Isle of Pines would be worth recognizing as a subspecies. The male differs from Cuban males in being paler on the cheeks with much more of a buffy tinge there; the female is paler throughout than in Cuban examples, and considerably lighter in color below. The iris in this form is light brown.

94. *Corvus nasicus* Temm. "CAO."—The Crow was found sparingly, usually in pairs, near the Ciénaga. It is a restless bird and has a habit, when one comes within sight, of hovering over one's head high in air screeching and scolding continuously. The natives sometimes tame the Crow and teach it to say a few words. The iris is dark red.

Five specimens, adults of both sexes, were taken at La Vega and Pasadita in April and May.

95. *Progne cryptoleuca* Baird. "GOLONDRINA."—Not common in the Isle of Pines. It was seen several times, but no nesting place was found. Palmer and Riley found small colonies in the pines at Managua.

96. *Petrochelidon fulva* (Vieill.). "GOLONDRINA."—Like the Martin, the Cliff Swallow was not found nesting in any region visited by Zappey. It was seen flying several times. Palmer and Riley found it abundant in the lowlands near Nueva Gerona.

97. *Mniotilta varia* (Linn.).—Recorded from the island by Poey, and seen on the March, 1902, trip.

98. *Compsothlypis americana* (Linn.).—Recorded from the island by Poey, and also seen in March, 1902. Without specimens it is of course impossible to tell to which subspecies, as now recognized, this record applies.

99. *Chrysocantor petechia gundlachi* (Baird).—The Mangrove Warbler was not observed in the Isle of Pines on either trip, though it was common at the opposite coast of Cuba at Batabano where a series of specimens was taken while waiting for a vessel to sail for the island.

It is recorded from the island by Poey and by Cory.

100. *Dendroica cærulescens* (Gmel.).—Recorded from Isle of Pines by Poey and by Cory and not uncommon in March, 1902. None were seen in 1904.

101. *Dendroica virens* (Gmel.).—First recorded from the island by Poey, and later Gundlach says that he took his first specimen of this species in the Isle of Pines in January, 1855.

102. *Dendroica dominica dominica* (Linn.).—This is another species recorded by Poey and found in March, 1902, but not seen in 1904.

103. *Dendroica discolor* (Vieill.).—Given by Poey from Isle of Pines, but not observed on either of the trips made to the island by Zappey.

104. *Dendroica palmarum palmarum* (Gmel.).—Recorded from Isle of Pines by Cory and found there in March, 1902, but not on the second trip.

105. *Seiurus noveboracensis* (Gmel.).—Recorded by Poey and seen in March, 1902.

106. *Teretistris fernandinæ* (Lembeye). "CHINCHILETA."—This beautiful little ground warbler inhabits the thick, dense woods and is probably commoner than it appears to be. It was not often seen, however.

Three specimens, two males and a female, were taken at Pasadita and Callebonita, in May and June. These are precisely like Cuban ones.

107. *Geothlypis trichas* (Linn.).—Recorded by Poey from Isle of Pines. The subspecies to which this record applies is of course somewhat uncertain. Ridgway identified a series of birds taken in western Cuba by Palmer and Riley as *ignota*, and all

birds from eastern Cuba as *brachidactyla*. Judging from this the form wintering in the Isle of Pines should be *ignota*.

108. *Setophaga ruticilla* (Linn.). — Recorded by Poey, and found quite commonly in March, 1902. None were observed in April, 1904.

109. *Holoquiscalus gundlachii* (Cassin). "CHICHINGUACO." — Common in more open country, pastures, and ploughed fields. When the natives are ploughing, the grackle, often in great numbers, follows the plough to pick up grubs and the like that are turned up. It also, like the Ani, alights on the backs of horses and cattle to pick off ticks. The male, owing to the vertically placed feathers in the tail, presents a curious appearance when on the wing.

Nine specimens, both sexes, were taken, all at Santa Fé in April and May.

These skins average a little smaller with smaller bills than Cuban ones, and are, perhaps, a trifle duller in coloration, but in all these points Cuban birds vary, and there does not appear to be any real character by which the Isle of Pines grackle can be distinguished.

The series measures as follows: —

No.	Sex.	Wing.	Tail.	Tarsus.	Exposed culmen.
13,274	♂ ad.	137	120	36	33
13,275	♂ ad.	139	122	37	33.5
13,276	♂ ad.	140	128	36	33.5
13,277	♂ young ad.	135	115	35.5	34
13,278	♂ young ad.	131	107	34.5	33
13,279	♂ young ad.	136	110	37	33
13,281	♀ ad.	135	107	35	31.5
13,282	♀ ad.	123	102	32	28

110. *Ptiloxena atrovioacea* (d'Orb.). "TOTI." — Probably a rare bird in the Isle of Pines as none were observed. The natives, however, know the "Toti" from the "Chichinguaco." It is recorded from the island by Poey and by Gundlach.

111. *Icterus hypomelas* (Bonap.). "SOLIBIA." — Common, especially among the pines. The oriole feeds a good deal among the flowers of various shrubs and trees, and its head is often daubed with juice and pollen from these.

Fourteen specimens, adults of both sexes and young including nestlings, were taken at Jucaro, Hospital, Callebónita, and Santa Fé in April, May and June. In birds from the Isle of Pines the yellow color of rump, thighs, and wing-coverts is a little paler than in Cuban examples, as is also the brownish yellow of under tail-coverts and anal region, with less of this color and rather more black than in Cuban specimens; but these differences are not very tangible and the Isle of Pines bird is not different enough to be formally separated as a subspecies.

112. *Agelaius assimilis* Lembeye.¹ "TOTI LA CIENAGA." — During the period spent near the Cienaga — April and May — all the birds of this species, that probably at some time of year scatter through the swamp to breed, were congregated in one flock that kept to some large trees at the edge of the Cienaga. The breeding season was not near at hand as the testes of the males were not enlarged, neither had it just passed as no very young birds were seen.

The notes of this species resemble those of the common Red-wing (*Agelaius phoeniceus*) but are lower and more wheezy, sounding, when a number are calling together, much like the chirping of insects.

In the adult male the wing is colored like that of *A. phoeniceus floridanus*, but younger males have the shoulder black, as in the adult female, except that some of the feathers are irregularly tipped and spotted with red and tawny, the amount of these colors varying much, from individuals with scarcely any to those that begin to show the characteristic markings of the adult.

Of all the Icteridæ this is probably one of the rarest and most local species, being known only from the Zapata Swamp in Cuba and the Cienaga in the Isle of Pines.

Seven specimens, both sexes, were taken, all at the edge of the Cienaga in April.

113. *Sturnella hippocrepis* (Wagler). "SABANERO." — The Meadowlark is common in pastures and fields and in the edge of the pine woods, and is very tame and unsuspicious.

Six specimens, adults of both sexes, were taken at Santa Fé,

¹ Ex Gundlach, MSS.

Jucaro, and Callebón in April and May. These are similar to Cuban specimens, although they average more yellow on the thighs. Some Cuban skins, however, have the thighs nearly as yellow as Isle of Pines birds.

114. *Dolichonyx oryzivorus* (Linn.). — A casual migrant to the Isle of Pines, recorded by Cory and by Gundlach, but not observed on either trip.

115. *Spindalis pretrei pinus* subsp. nov.

"CABRERO."

Type from Santa Fé, Isle of Pines, adult male, no. 13,317, Coll. of E. A. and O. Bangs. Collected April 18, 1904, by W. R. Zappey.

Characters. — Similar to true *Spindalis pretrei* (Lesson) of Cuba, but considerably larger with a larger bill. There is also a slight average difference in color, the male of the new species being rather paler and more purely yellow, less rufous-orange and tawny-orange, on nuchal collar, lower rump, and chest, than in Cuban examples; and the black cap extends rather farther backward, encroaching more upon the yellow of the nape band. The female appears not to differ in color, though our specimens are slightly paler and grayer than Cuban ones, but they were all taken in spring and early summer, whereas the Cuban examples we have compared them with were shot in December. The difference therefore is probably seasonal.

Measurements: —

No.	Sex.	Wing.	Tail.	Tarsus.	Exposed culmen.
13,311	♂ ad.	75	57.5	18.5	12.5
13,312	♂ ad.	74.5	57	18	12.5
13,323	♂ ad.	76.5	59	18.5	13
13,314	♂ ad.	77	57.5	18	12
13,315	♂ ad.	71	54	19	12
13,316	♂ ad.	73.5	56.5	19	12
13,317	♂ ad.	75	59	19.5	12
13,318	♂ ad.	75.5	60	18.5	12.5
13,319	♂ ad.	72.5	55	18	12
13,320	♂ ad.	73	57	19	11.5
13,321	♂ ad.	72.5	57	18	12

No.	Sex.	Wing.	Tail.	Tarsus.	Exposed culmen.
13,322	♂ ad.	75	57.5	18	12
13,310	♀ ad.	69	54	17.5	12
13,313	♀ ad.	68	52	17	12
13,324	♀ ad.	69	50	17.5	12
13,325	♀ ad.	71	55.5	18	12
13,326	♀ ad.	68	53	17.5	12
13,327	♀ ad.	67	53.5	18	11
13,328	♀ ad.	69	52	18	12.5
13,329	♀ ad.	67	50	17	12
13,330	♀ ad.	72	52	18.5	11.5

The Spindalis is a conspicuous and rather common bird in the Isle of Pines, frequenting the pines and a tree (name not known) that bears a pink blossom. Both the males and females sing, the song being a low, weak warble.

Twenty-one specimens, adults of both sexes, were taken at Santa Fé, Jucaro, Callebónita, Pasadita, and San Juan, in April, May, and June. These differ from Cuban examples, as has been pointed out by Ridgway in *Birds of North and Middle America*, in larger size and bigger bills, and in addition show a slight average difference in color.

116. *Tiaris olivacea olivacea* (Linn.). "TOMEQUIN DE LA TIERRA." — A rather common bird in the Isle of Pines, in the brushy country, and particularly fond of thorn bushes, and one species of palm upon the berries of which it feeds.

Nine specimens, adults of both sexes, were taken at Santa Fé and Callebónita in April, May, and June.

Ridgway in *Birds of North and Middle America* (Part I, p. 531, footnote) speaks of the slightly larger size and duller colors of the male Grassquits from Cuba, Grand Cayman, and Little Cayman as compared with those from Haiti and Jamaica. The series from the Isle of Pines bears out both peculiarities — larger size of the males and duller colors — but the differences are very slight and hardly sufficient to base a new form upon. The specimens measure as follows : —

No.	Sex.	Wing.	Tail.	Tarsus.	Exposed culmen.
13,301	♂ ad.	49	37.5	15.5	9
13,303	♂ ad.	47.5	37.5	16	9
13,304	♂ ad.	49.5	38	15.5	9.5

No.	Sex.	Wing.	Tail.	Tarsus.	Exposed culmen.
13,306	♂ ad.	51.5	40	16	9
13,307	♂ ad.	50.5	39	15.5	9
13,308	♂ ad.	50.5	38.5	15.5	9
13,309	♂ ad.	52	41	15.5	9.5
13,302	♀ ad.	47	37.5	15	9
13,305	♀ ad.	47	36	15.5	8.5

117. ? *Tiaris canora* (Gmel.). "TOMEQUIN DEL PINAR."—Under the name *Passerina collaris* Vig., a synonym of the Melodious Grassquit, Poey recorded this bird from the Isle of Pines. Cory also gives the species from the island, but may have taken it directly from Poey. Poey does not include the common Yellow-faced Grassquit in his list, and we consider this a very doubtful record probably due to confusion of names.

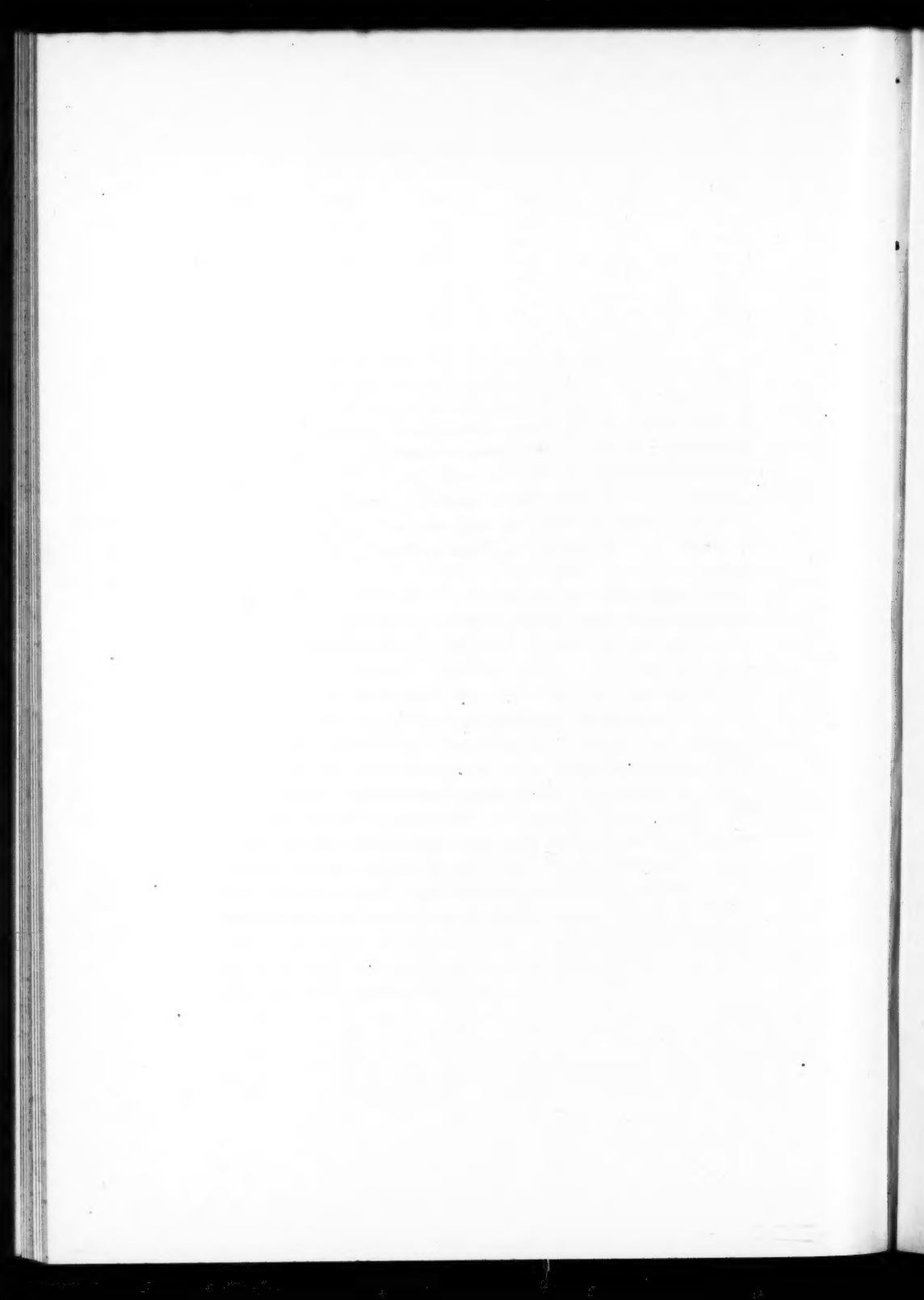
At all events, it must be very rare, as nothing was seen or heard of it in the Isle of Pines by Palmer and Riley or by Zappey.

118. *Melopyrrha nigra* (Linn.). "NEGRITO."—The Cuban Bullfinch appears to be restricted in the Isle of Pines to the dry, brushy country south of the Cienaga and even there is not at all common.

One male was taken at Puerta del Este, on April 29.

119. *Passerculus sandwichensis savanna* (Wilson).—The Savanna Sparrow was taken in March, 1902, but on the second trip to the island, beginning in April, none were seen.

120. *Coturniculus savannarum passerinus* (Wilson).—The Yellow-winged Sparrow was also found in March, 1902, and was not observed during the 1904 trip. None appear, therefore, to breed in the Isle of Pines, and those seen in March, 1902, undoubtedly were northern birds. There is, however, a resident breeding race in Cuba, as well as northern birds that pass the winter there.



STUDIES ON THE PLANT CELL.—V.

BRADLEY MOORE DAVIS.

SECTION IV. CELL UNIONS AND NUCLEAR FUSIONS IN PLANTS.

THE forms of cell unions and nuclear fusions in plants fall into two groups: (1) those which obviously have no sexual significance attached to them, and (2) those which are evidently sexual acts. But apart from these simple divisions there are some very interesting conditions in which it is far from easy to determine whether certain events have a sexual significance either physiologically or phylogenetically. The real test of such problems should lie in the evolutionary history of the processes involved, for every sexual condition in plants has probably developed in obedience to the same physiological demands and in an essentially similar manner. However, we cannot apply the evolutionary test in many cases where we have little evidence of the developmental history of the group and such forms must rest for the present as unsolved problems. We shall treat them in special connections later in the paper.

The material of this section will be presented under the following heads:—

1. Protoplasmic connections between cells (plasmodesmen).
2. Sexual cell unions and nuclear fusions.
3. Asexual cell unions and nuclear fusions.

1. Protoplasmic Connections between Cells (Plasmodesmen).

It has been known for a great many years that the walls between the cells in some plant tissues and more especially between the cells of filaments in certain thallophytes were crossed by delicate strands of protoplasm so that contiguous protoplasts were not entirely separated from one another. This fact

offers at once many interesting possibilities of explaining the close association of many cells and tissues, not alone in delicate dynamic interrelations but even in the exchange and distribution of food material and other products of metabolism. It makes possible the conception of the plant body as a finely adjusted community of protoplasts intimately and sensitively related to a great degree in all parts, a view very different from the old idea of a cell republic. As might be expected, these speculative possibilities were conceived and expressed by such leaders as Hofmeister, Nägeli, Sachs, and Strasburger long before the detailed study of protoplasmic connections gave the mass of evidence upon which have been based the more elaborate conceptions of recent years.

The most obvious protoplasmic connections between cells may be found in the thallophytes where as in the Rhodophyceæ, Volvox, and in certain fungi, the cells in younger structures may be observed under comparatively low magnification to be united by strands of protoplasm so broad as to quite exclude them from the category of fibrillæ. Some of these structures are so conspicuous that it is surprising that more was not made of them by early writers and that they have not been more extensively investigated recently. The greater part of the papers have been on the very difficult phase of the subject, the structure of pores and pits in the tissues of higher plants. The literature treating of protoplasmic connections is too extensive to be given detailed treatment in the compass of this paper. The best review of the subject is that of Strasburger (:01), supplemented by the more recent paper of Kienitz-Gerloff (:02).

The earlier papers on the protoplasmic connections in higher plants, following the establishment of perforations of sieve-plates by Sachs and Hanstein, appeared during the years just preceding and following 1880. Thus Tangl ('79-'81) described very clearly the communications between the endosperm cells of *Strychnos nux vomica* and Phoenix (see Fig. 16, a). Tangl noted the resemblance of the complex of connecting threads to the arrangement of spindle fibers associated with the simultaneous division of the protoplasm in the endosperm but was cautious in assuming a relationship, suggesting that the resemblance might be superficial.

Strasburger ('82, p. 246) discussed the permeability of cell walls and Gardiner ('88) gave a general treatment of the subject without, however, any figures to illustrate his conclusions. Gardiner discovered for a large number of forms in a wide variety of families that the pit membranes were frequently pierced by protoplasmic fibrils and that in some cases the fibrils traversed the entire thickness of the cell wall. A more detailed study with better methods, supplementing his former work and accompanied by figures, was published by Gardiner, in 1898, this paper forming an important contribution to the subject. Gardiner (:00) announced himself strongly in favor of the view that the protoplasmic connections between cells were derived from spindle fibers of nuclear figures concerned with each cell division, a possibility which had been suggested by previous writers (Tangl, '79-'81; Russow, '83).

Kienitz-Gerloff ('91) gave an excellent account of the protoplasmic connections in a number of forms, some of them pteridophytes, but especially for *Viscum album*, and followed the history of the wall formation, showing that the spindle fibers disappeared completely before the development of the connecting strands of protoplasm. Kuhla (:00) followed Kienitz-Gerloff with more extended studies on the same form, *Viscum album*, tracing the protoplasmic fibrils between the cells in all the chief tissues and establishing the protoplasmic connections throughout the individual to an extent that was not known before. Hill (:01) described the structure of the sieve-tubes of *Pinus*, dealing especially with the formation of callus and the conversion of the connecting threads of protoplasm into strings of slime. An excellent review is also given of the work of Russow and others, particularly upon sieve-tubes. Kohl ('97) describes clearly protoplasmic connections between the cells of moss leaves.

A classification of protoplasmic connections was suggested by Kohl (:00) who distinguished between the solitary state when each fibril pierces the cell wall independently of its neighbors (Fig. 16, a and b) and a grouped condition when a number of fibers arise close together at the bottom of a pit and pierce the pit-membrane or middle lamella in a spindle-shaped arrangement,

reminding one of the central spindle of a mitotic figure (Fig. 16, c). In general the two types of protoplasmic connections are not found together in the same cell or tissue.

A new point of view was introduced into the discussion by the very important paper of Strasburger, in 1901. He considered the protoplasmic connections as sufficiently clearly differentiated structures to rank as organs of the cell and proposed for them the name plasmodesmen. Strasburger in agreement

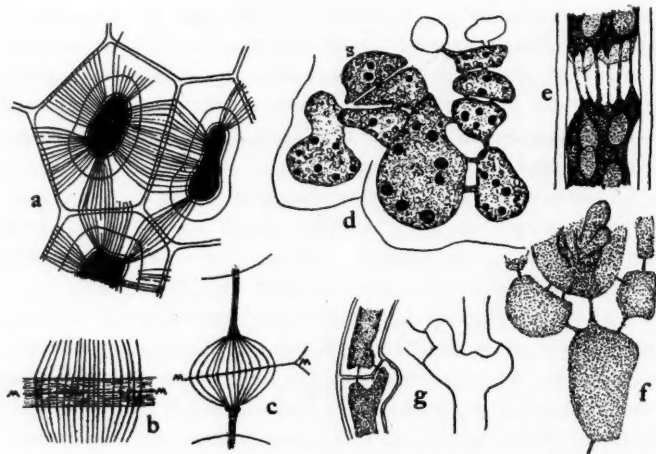


FIG. 16.—Protoplasmic connections between cells of plants. *a*, endosperm cells of *Strychnos nuxvomica*; *b*, details of the solitary fibers in the same form, (*m*) middle lamella; *c*, grouped fibers at bottom of pit in endosperm of *Phytolapha* and crossing the pit membrane in a spindle-shaped figure; *d*, cell connections around the sporophytic portion of a developing cystocarp of *Champia*, (*s*) sporophytic elements; *e*, fibers between cells of *Cladophora*; *f*, cell connections around the ascogenous elements in *Laboulbenia*; *g*, clamp connections in *Pleurotus* (*a*, after Tangl, '79-'81; *b* and *c*, Kohl, :00; *d*, Davis, '96 b; *e*, Kohl, :02; *f*, Thaxter, '96; *g*, Meyer, :02).

with Kienitz-Gerloff opposed the view that the plasmodesmen were in any way derived from or related to the spindle fibers associated with the formation of cell plates. He believed them to be developments of the outer plasma membrane as he likewise considers the cilia in certain zoöspores (see account of zoöspore and sperm in Section III, *Amer. Nat.* vol. 38, pp. 571, 576, 1904). Strasburger also holds that pores are formed in the cell walls by the formative activities around plasmodesmen. A

recent short paper by Michniewicz (:04) describes clearly the plasmodesmen in *Lupinus*, especially in their relation to masses of intercellular protoplasm which are discussed at the end of this portion of the section.

It is not clear whether all protoplasmic connections may be considered in the same class, as Strasburger would have us believe, or whether there may not be some confusion between the broader cell connections which are especially conspicuous in the thallophytes and certain tissues (sieve-tubes, laticiferous vessels), and the delicate protoplasmic fibrils (plasmodesmen) so general throughout all tissues of higher plants. As is well known, the cells in actively growing regions of the red algæ are connected by broad strands of protoplasm that are obviously left by the cleavage furrow which constricts the protoplasm of daughter cells but does not entirely separate them. These openings may become partially blocked in older portions of the plant by the deposition of material so that the connections are finally fibrillar but they frequently remain open for long periods, particularly in regions where the nutritive processes are active as during the development of cystocarps. At this time new fusions may be developed between neighboring cells (auxiliary cells) so that they become connected in an elaborate network around the cells or filaments (sporophytic) that develop the carpospores (Fig. 16, d). The Phæophyceæ also furnish frequent illustrations of connecting fibrils especially in the Fucales and Laminariales where the cells of internal filaments are sometimes connected by conspicuous strands. Certain elongated filaments which traverse the central region of the larger brown algæ show a complicated group of fibrils that strikingly resembles the protoplasmic connections piercing the sieve-plates of higher plants. Broad protoplasmic connections are conspicuous between the cells of some of the filamentous Cyanophyceæ (*Stigonema*, *Tolypothrix*) and in the Chlorophyceæ have been reported for some species of *Cladophora* (Kohl, :02; Fig. 16, e) and for *Chætopeltis*, one of the Mycoideæ. They do not seem to be present in the Conjugales as was at first reported by Kohl ('91) whose cells show a great degree of physiological independence. In *Volvox*, studied by Meyer ('96), each cell of the

sphere is connected with its neighbors generally by six strands of protoplasm, only a few of which could possibly be left by the successive cell divisions. The majority must have developed as outgrowths from the plasma membrane of the cell.

Numerous instances of cytoplasmic connections among the fungi have been reported by many authors. A general review of the subject is presented by Kienitz-Gerloff (:02) and in a lengthy paper of Meyer (:02). The protoplasmic connections fall into two groups: (1) those that remain in the center of the wall after a cell division, and (2) the lateral unions and clamp connections which are developed entirely independently of cell division. Connections of the first type, *i. e.*, those between daughter cells, appear to be very general in the Ascomycetes and Basidiomycetes and are essentially similar to the strands between cells of the Rhodophyceæ. They are especially well illustrated in members of the Laboulbeniaceæ (Thaxter, '96; see Fig. 16, f). In the second group are the clamp connections (Fig. 16, g), characteristic structures of the tissues of fleshy forms of the Basidiomycetes, and the lateral unions between cells of closely entangled hyphæ which are well known in a number of forms and have been followed in cultures from germinating spores. It is probable that the fusions between sporidia in the smuts are also of this class, although De Bary and others have attached sexual significance to the phenomenon (especially as illustrated by *Tilletia*). Harper ('99a) has studied the fusions of the conidia of *Ustilago* and finds that they concern the cytoplasm alone. However, Federley (:03-:04) has reported a nuclear fusion in one species (*Ustilago tragopogonis pratensis* Pers.) but states that others agree with Harper's account. Extensive experiments of Brefeld have shown that the fusions of sporidia depend largely upon the character of the nutrient media and are less likely to occur when the conditions are favorable. He considers the fusions as purely vegetative processes comparable to the unions of germ tubes of spores (*e. g.*, *Nectria*, *Sclerotinia*, *Rhyaromyces*, etc.) into a common mycelium and to the connections between hyphæ of Basidiomycetes. Recent studies of Blackman (:04 a) indicate also that sexual processes should not be expected at this period in the life his-

tory of smut or rust. One of the best discussions of cell fusions in the fungi is that in Harper's paper ('99a), noted above.

Although most of the protoplasmic connections in higher plants are of the fibrillar character there are some notable illustrations of broad openings between cells, even more conspicuous than those in the red algæ. Such may be found in the pores of sieve-plates traversed in their early stages by strands of protoplasm that later disappear, and even better illustrations are the unions between cells composing laticiferous vessels. But the most interesting conditions are those associated with the nutrition of the eggs of certain cycads. Goroschankin ('83) first noted for the cycads pores or canals in the egg-wall of *Ceratozamia* and described communications between the protoplasm of the enveloping cells of the jacket and the egg. The subject is closely associated with the explanation of the proteid vacuoles in the eggs of gymnosperms which Arnoldi believed to be nuclei that had migrated from the surrounding cells. The conclusions of Arnoldi have not been sustained (see Sec. III, *Amer. Nat.*, vol. 38, pp. 591, 592, 1904) but the presence of pores in the egg-wall of gymnosperms is likely to prove very general with further investigation. A recent paper by Miss Isabel Smith (:04) gives an account of haustoria-like processes from the egg of *Zamia* which pass through the pores of the egg-wall into the cells of the jacket, where they are in direct contact with its protoplasm. These pseudopodia-like processes of the egg apparently absorb material from the cells of the jacket as is indicated by the character of their staining and the streaming movement towards them of the protoplasm in the jacket cells. The relation of the plasma membrane of the processes from the egg to that of the jacket cells is not clear but probably they are merely in contact and not in open communication. The ovules of cycads seem to offer an especially favorable subject for the study of pore formation and the intimacy of protoplasmic connections between cells.

It seems very clear that the cytoplasmic connections in the Rhodophyceæ, Volvox, fungi, and between the egg and jacket cells of cycads involve very much more substance than is generally present in the delicate fibrillæ of higher plants. Meyer

(:02, pp. 167, 168) seems justified in emphasizing their resemblance to pseudopodia rather than to any other structure of the cell. If they should finally be connected by intergradations with the exceedingly fine plasmodesmen of Strasburger, there would stand at one end of the series structures so thick as to be composed of a plasma membrane containing much cytoplasm in the interior and behaving like haustoria or pseudopodia and at the other end delicate fibrillæ. Viewing the problem of their relationships from the lower plants upwards, it is very difficult, if not impossible to follow Strasburger's theory that all cytoplasmic connections (plasmodesmen) are related to developments from the plasma membrane similar to cilia. They seem to be more of the nature of processes put out from the cytoplasm and when necessary penetrating cellulose walls probably in response to chemotactic stimuli since they are most conspicuous when metabolic activities are obviously important (*e. g.*, nourishment of the egg in gymnosperms and sporophytic generation of the red algæ).

In method of development we have seen that protoplasmic connections fall into two classes: (1) those that represent the incomplete separation of daughter cells, and (2) those that result from the coming together or fusion of protoplasmic outgrowths. The types of the first group are always in the beginning open communications which later may become largely or wholly closed; types of the second group may result in broad cytoplasmic fusions (*e. g.*, many fungi) but there is evidence that in many cases, especially among the higher plants, the two processes only come in contact so that the plasma membranes are applied to one another but do not actually unite. It does not seem probable that the two methods of development or the presence or absence of intimate protoplasmic union indicate a different kind of structure. They are more likely to be only varied responses to the demands for a more or less close association of neighboring cells. Broad communications are especially characteristic of regions where there is evidently an extensive demand for the nourishment of a cell or tissue, as in the eggs of the cycads or the cystocarp of the red algæ.

The functions of protoplasmic connections are probably vari-

ous. It is evident that they bind the whole plant body into a cell complex capable of very delicate interrelations. It is natural that physiologists, Pfeffer and others, should associate the structures with the phenomena of irritability as the paths over which stimuli may be transmitted from cell to cell and tissue to tissue. Several writers have reported their presence in unusual numbers in irritable structures of plants. The subject is discussed in great detail by Strasburger (:01, p. 533).

Besides conducting stimuli, there is much evidence that material may be transferred in solid or semifluid form by the protoplasmic connections from cell to cell and that in some instances there is actually a movement or flow of protoplasm. It is even known that nuclei may pass from cell to cell through pores in the wall, especially after some shock, as in the neighborhood of wounds (Miehe, :01), or when temperature is suddenly raised (Schrammen, :02). This literature and other references are discussed by Koenicke (:01; :04). A flow of protoplasm between neighboring cells of hyphæ has been reported by Reinhardt ('92) and Charlotte Ternetz (:00). That nuclei may pass through very small space is shown in the development of spores in the Basidiomycetes and in the growth of haustoria from the cells of hyphæ (Smith, :00). There are many forms known, especially among the thallophytes, where the communications between cells are so broad as to admit of a very free circulation of their contents. Such conditions are especially well illustrated in tissues around the developing cystocarps of the Rhodophyceæ and the ascocarp of the Ascomycetes, both structures apparently sporophytic in character and dependent to a great degree upon the gametophyte as a host. It is believed that the vitality of protoplasm in sieve tubes, whose nuclei have degenerated and disappeared, is maintained through protoplasmic connections with neighboring cells and especially the companion cells, when present. Of course where an actual circulation of protoplasm is established between cells or tissues there is made possible a distribution of the products of metabolism in solid form that is very different from the usual diffusion in tissues through cell walls and plasma membranes.

It seems probable that there are really two forms of protoplasmic connections between cells in plants: first, those so intimate that the plasma membranes are pierced and become continuous openings inclosing a strand of granular cytoplasm within; and second, those in which the plasma membranes are merely applied to one another without open communication. The second form comprises the most delicate connecting fibrillæ, structures so fine that their minute structure is not understood and we do not know how intimate may be the application of the fibrillæ to one another or to the surface of the cells. These are the typical plasmodesmen of Strasburger which he considers as organs of the plasma membrane, kinoplasmic in character, and compares to cilia. The broad connections of the first group have exactly the structure that would be expected of fused pseudopodia, as Meyer pointed out. Whether the two types insensibly grade into one another or whether each is a development by itself is a problem of considerable interest, for if the former possibility prove true, Strasburger's conception and classification of plasmodesmen as organs of the cell will hardly seem justified.

When protoplasmic connections become so broad that cytoplasm flows or surges from one cell to another, an actual transfer of nuclei sometimes takes place. Such conditions may illustrate simply one extreme of the series of protoplasmic connections that we have just discussed, but many of them introduce some complexities, mainly through a certain resemblance to sexual processes, so that they should be treated apart from general protoplasmic connections. Some of them will be described later under the head of "Asexual Cell Unions and Nuclear Fusions."

Closely associated with protoplasmic connections is the interesting subject of intercellular protoplasm which is receiving some attention at present. The last papers are by Kny (:04) and Michniewicz (:04) who are studying conditions in the seed, especially of *Lupinus*. By various reactions and physiological studies, Kny has established an apparent identity of nature between an intercellular substance, sometimes with starch inclusions, and the cytoplasm of the neighboring cells. He considers this substance to be intercellular protoplasm, that is,

protoplasm outside of the cell walls, but connected with the cytoplasm within through fibrillæ. The intercellular protoplasm is thus conceived in organic connection with nucleated cells and from the studies of Townsend ('97) we know that non-nucleated protoplasm may live so long as it is united with nucleated, even though it be by very delicate fibrillæ. Michiewicz (:04) confirms Kny's conclusions for *Lupinus* and gives a very clear account of the fibrillæ which connect the masses of intercellular protoplasm with neighboring protoplasts. These studies make clearer a number of observations of several investigators (Sauvageau, Buscalioni, Schenk, Magnin, Strasburger, and others) who have noted similar conditions in the tissues of higher plants which are being investigated in detail by Kny. Some of the lower unicellular forms likewise exhibit an extracellular surrounding film or envelope, which may also be of a protoplasmic nature and consequently in the same position in relation to the protoplast as intercellular protoplasm. Thus it has been known for many years that the cells of the Peridinales, diatoms, and desmids possessed extracellular material, which some authors have considered in the nature of slimy excretions but others — Schutt ('99; :00a; :00b), Hauptfleisch ('88; '95), Müller ('98-'99) — have regarded as protoplasmic in character. Since the cell walls in these forms are known to possess pores, such extracellular substance must be in close association with the cytoplasm of the cell and it is not at all difficult to conceive of it as a part of the protoplasm. Some of the peculiar creeping movements of the diatoms and desmids are perhaps explicable upon these facts.

2. Sexual Cell Unions and Nuclear Fusions.

The test of a sexual act must lie with the history of the elements which fuse. If these are shown by their morphology and developmental history to be sexual cells or gametes then their fusion becomes a sexual process. There are cell and even nuclear fusions which have the physiological appearances of sexual acts but cannot be so considered because the elements concerned have plainly no relation to sexual cells, which are

developed at other periods of the life history, or to the primitive conditions always found with the origin of sex. These exceptional processes will be collected and described under the heading "Asexual Cell Unions and Nuclear Fusions," following this portion of the paper.

The union of gametes is generally termed fertilization. The evolution of the sexual process always tends towards a differentiation of the two sexual cells, one becoming more richly stored with food material and containing more protoplasm than the other. This latter gamete is always considered the female and is said to be fertilized when the male gamete, either as a motile sperm or reduced simply to a sperm nucleus generally with some accompanying protoplasm, fuses with it. The most evident morphological feature of fertilization is the close union of the gamete nuclei so that the chromosomes of both enter into the mitotic figure with which the new generation begins.

We shall not discuss the various forms of gametes nor their habits in different types of sexual reproduction. They have been described in two articles by the author on the origin and evolution of sex in plants (Davis, :01; :03). A detailed account of the sexual reproduction of well known types throughout the plant kingdom has been recently published by Mottier (:04b) under the title "Fecundation in Plants" a term which he prefers to fertilization. This paper gives in English the most extensive summary of our knowledge of the subject up to the date 1902 and will be read with especial interest as the most available expression in English of Strasburger's general views on the significance of the events connected with sexual reproduction.

A recent paper of Guérin (:04) is confined to an account of fertilization in the phanerogams which are treated in considerable detail. His discussion of double fertilization and parthenogenesis is of especial interest and will be taken up later.

Our purpose is to divest from the events of sexual cell unions and nuclear fusions all secondary and unessential processes and to outline, as are now understood, the fundamental phenomena. And to make the subject more plain we shall try to compare in their essentials the events of fertilization in plants with those

in animals. Probably the most important feature of fertilization is the close union of the gamete nuclei through which the chromosomes of both enter into the first mitotic figure of the new generation. It involves the organization of the first cleavage spindle, which inaugurates the new generation, and the history of the paternal and maternal chromosomes of the gametes at this time when the number becomes doubled.

Several zoölogical papers have developed in the past few years some very important conclusions concerning the individuality of the paternal and maternal chromosomes, as maintained during the fusion of the gamete nuclei and in the formation of the first cleavage spindle. It has been generally believed for some time — see general review in Wilson (:00, p. 204) — that the fusion of gamete nuclei did not involve a coalescence of the chromosomes but that both paternal and maternal chromosomes maintained complete independence of one another and that all entered into the first cleavage spindle as structures quite as distinct as when formed during spermatogenesis and oögenesis. Häcker and Rückert have shown for *Cyclops* that the gamete nuclei divide side by side in the first mitosis following fertilization, and Häcker followed these double nuclei as far as the 16-celled stage when they were still distinct from one another. A few notable investigations of recent years have identified chromosomes accurately as maternal and paternal not only in the first cleavage spindle but through certain succeeding mitoses and finally at the period of gametogenesis when sperm and egg were again formed. The above principles have been established chiefly through a series of papers of Montgomery, the chief being a lengthy investigation of 1901, and contributions of Sutton (:02; :03) and Moenkhaus (:04). They have given us clear evidence that the chromosomes not only maintain their complete individuality throughout successive generations but are distributed with gametogenesis and fertilization in various possible combinations that can be expressed by mathematical formulæ furnishing the basis for certain ratios that approximate the teachings of Mendel's law. We shall have occasion to refer to these in Section V when the subjects of gametogenesis, reduction of chromosomes, and hybridization will be discussed.

The same principles have been established in plants by recent investigations, some of which deal with oögenesis and spermatogenesis and will be specially treated in the Section V while others treat of the behavior of the chromosomes when the gamete nuclei fuse and the sporophyte generation begins its development. The latter conditions concern the present discussion.

The history of the chromosomes in plants at the time when the gamete nuclei fuse (fertilization) is most accurately known for the pine. The last paper upon this type (Ferguson, :04) is very complete. Miss Ferguson gives a beautiful series of figures, some of which we have reproduced. The sperm nucleus comes in contact with the egg nucleus and sinks into the latter so that it lies in a depression, but as noted by Blackman ('98), it does not penetrate the membrane of the egg nucleus (Fig. 17, a). Both gamete nuclei thus lie side by side occupying approximately the same space formerly filled by the female. Each shortly gives evidence of preparation for the mitosis following fertilization (first cleavage spindle). The chromatin of the egg nucleus collects in a spirem, very close to the sperm, occupying a relatively small portion of this large female nucleus (Fig. 17, b). The chromatin of the sperm nucleus also takes position as a spirem on the side nearest its companion chromatin of the opposite sex. The remaining space of each nucleus is filled with a granular reticulum of a linin nature. At this time the amount of linin is extraordinarily large in proportion to the chromatin, suggesting that some of the latter substance has become changed to the former. Soon, delicate fibrillæ appear around the two spirems growing outward in various directions and finally crossing from one nucleus to the other. At the same time the two nuclear membranes become less distinct and shortly disappear. Thus the maternal and paternal spirems come to lie in a common area filled with delicate fibrillæ which run out to the granular cytoplasm that lay around the two gamete nuclei (Fig. 17, c). It should be especially noted that at no time in this history has there been a resting nucleus including both maternal and paternal chromosomes within a common nuclear membrane. The fusion of the gamete nuclei has only come with the actual formation of the first cleavage spindle.

The fibrillæ organize a multipolar spindle which is very variable in form, sometimes with broad poles of a multipolar diarch (Fig. 17, d) and at other times almost as pointed as in a typical bipolar spindle (Fig. 17, e). There are, of course, no centrosomes and the entire spindle is essentially of intranuclear origin. The history of its development recalls Miss Williams' account of the spindle in the pollen mother-cell of *Passiflora* (Sec. III, *Amer. Nat.*, vol. 38, p. 738, 1904). During spindle formation the spirems of the sperm and egg nuclei can be readily distinguished as was described by Blackman ('98) and Chamberlain

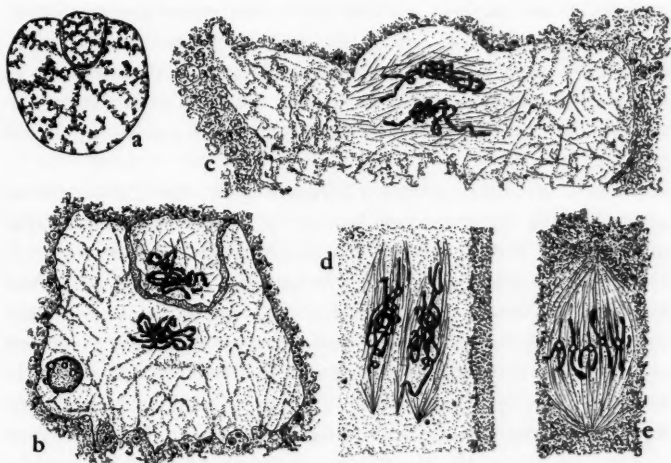


FIG. 17.—Fertilization in *Pinus strobus*. a, conjugating gamete nuclei; b, the gamete nuclei still separated, with nuclear membranes distinct, the maternal and paternal chromatin in two spirems; c, the nuclear membranes have disappeared and the two spirems lie close together surrounded by the fibrillæ which will organize the first segmentation spindle; d, prophase of the first segmentation spindle, of the multipolar diarch type, paternal and maternal spirems still distinct; e, metaphase of first segmentation mitosis, maternal and paternal chromosomes now indistinguishable, beginning to split in the middle region (after Ferguson, '04).

('99), but after the two sets of chromosomes are formed (twelve of each) the latter are brought so closely together at metaphase of mitosis that the paternal and maternal cannot be separated. All of the chromosomes are exactly alike and there is nothing in the form or size to distinguish one from another as certain

zoölogists have been able to do in some favorable animal types (Montgomery, Sutton, Moenkhaus). The chromosomes divide longitudinally in the usual way, the halves being drawn apart from the points of attachment of the spindle fibers (Fig. 17, e). It is clear that each daughter nucleus receives a full set of 24 daughter chromosomes, 12 of paternal and 12 of maternal origin, and that there is about an equal amount of chromatin from each sex.

It should be especially noted that in the process of fertilization in the pine there is at no time present what is generally called a fusion nucleus, *i. e.*, a single nucleus whose membrane incloses all the material of both male and female gamete nuclei. Such fusion nuclei, as we shall see, have been reported many times in other groups of plants than the gymnosperms where in many cases, however, detailed studies are very difficult and can scarcely be said to have even approached our knowledge of the pine.

Studies of other botanists indicate that the gymnosperms generally will show essentially the same conditions as in the pine. Thus Woycicki ('99) distinguished in *Larix* two groups of chromatin which he regarded as paternal and maternal. And Murrill (:00) states for *Tsuga* that the chromatin of sperm and egg remain separate, forming two spirems, and only after their segmentation into chromosomes are the two sets of structures brought together in the first cleavage spindle. Land (:02) figured the sperm nucleus of *Thuja* imbedded in a depression of the egg nucleus. Miyake (:03a) noted that the sperm nucleus of *Picea* became more or less imbedded in the egg nucleus while the nuclear membrane remained intact, and the same author (Miyake, :03b), reports similar conditions in *Abies*. Robertson (:04) figures the sperm nucleus of *Torreya* lying within a depression in the female and with a large amount of granular cytoplasm (kinoplasm) at the side. Coker (:03) states that the partition between the gamete nuclei of *Taxodium* "does not entirely disappear until immediately before the first division" although the two structures are closely united for some time previously while they pass to the bottom of the egg.

Lawson, studying *Sequoia* (:04a) reports gamete nuclei of

about equal size whose chromatin contents unite in a fusion nucleus to form a common network in which male and female elements cannot be distinguished. A similar condition obtains in *Cryptomeria*, according to Lawson (:04b), where a fusion nucleus is described in which paternal and maternal chromatin are mingled together in a nucleus that passes through a short period of rest before the development of the first cleavage spindle. In view of the work on *Pinus* I think it may safely be questioned whether in *Sequoia* and *Cryptomeria* the maternal and paternal chromatin really does form a common network in the resting fusion nucleus. The subject is one very difficult of study and demands more stages than Lawson seems to have followed.

Fertilization in the cycads is not as completely known as for the conifers. Webber (:01) figures the sperm nucleus of *Zamia* imbedded in the egg nucleus but quite distinct from it as in the pine but the further history leading to the development of the first segmentation spindle was not followed. On the other hand Ikeno ('98b) described in *Cycas* the formation of a cup-like depression in the egg nucleus to receive the sperm nucleus which was said to enter and fuse completely with the female and the same author (Ikeno, :01) reports a complete fusion of the gamete nuclei in *Ginkgo* and did not distinguish the paternal and maternal chromosomes during the formation of the first segmentation spindle. However it is probable that more detailed studies among the cycads and in *Ginkgo* will show a behavior of the sperm nucleus together with the paternal and maternal chromatin essentially similar to that of the conifers. All investigations among the cycads and in *Ginkgo* agree that cytoplasmic structures of the sperm (blepharoplasts, cilia, etc.) are left behind in the cytoplasm of the egg before the gamete nuclei unite.

Our knowledge of the details of fertilization in the angiosperms is surprisingly meager. The only account of the chromatin is that of Mottier ('98; :04b, p. 176) for *Lilium*. He describes and figures the two gamete nuclei as uniting with their chromatin in the resting condition. The nuclear membranes disappear at the surface of contact and the two nuclei

fuse into one. The nucleoli unite and so thoroughly does the paternal and maternal chromatin seem to be mixed in the resting condition that the fertilized egg nucleus can scarcely be distinguished from the unfertilized. There would seem to be then a fusion nucleus in the lily with the chromatin in the resting condition. The figures and brief accounts of other botanists indicate that similar conditions may be expected in other angiosperms. But no one has followed the chromatin in the fusion nucleus through its later history, during the organization of the chromosomes preparatory to the first mitosis following fertilization. It would be very surprising if paternal and maternal chromatin did not remain entirely independent of each other as in the pine. The detailed study of fertilization in the angiosperms presents a very attractive subject for investigation.

Some very interesting conditions of fertilization have been

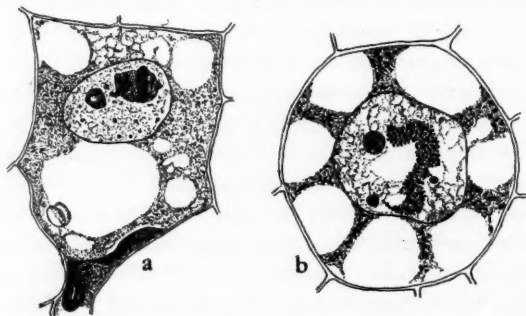


FIG. 18.—Fertilization in *Onoclea sensibilis*. *a*, sperm as a spiral band within the egg nucleus; *b*, later stage, the chromatin of the sperm much less condensed and more widely distributed in the egg nucleus (after Shaw, '98a).

described in the pteridophytes for *Onoclea* by Shaw ('98a), confirmed by Mottier (:04 a; :04 b), and for *Adiantum* and *Aspidium* by Thom ('99). In these forms the male nucleus after leaving in the protoplasm of the egg all of the cytoplasmic structures of the sperm (blepharoplasts, cilia, etc.) enters the egg nucleus as a more or less spiral body which stains deeply and is evidently chiefly or wholly chromatic in composition (Fig. 18). Within the egg the dense structure of the sperm nucleus becomes looser by the separation of the chromatin granules (Fig.

18, b) but the form of the sperm can be recognized for a long time. The chromatin of the egg nucleus is in a resting condition at this period and the densely packed mass of paternal chromatin is very conspicuous in the loose, delicate network of the female chromatin. The mitosis following fertilization does not occur for several days so that it is not easily studied and the organization of the first cleavage spindle with the history of the maternal and paternal chromosomes has never been followed. But it is clear that we have in the pteridophytes a true fusion nucleus containing for several days both maternal and paternal chromatin within the same nuclear membrane.

There is only one paper that gives any details of fertilization in the bryophytes, a contribution of Kruch ('90) on the liverwort, *Riella*, which seems to have been generally overlooked in recent literature. After the sperm enters the egg, a male nucleus is organized which increases in size until it is about equal to the egg nucleus. The chromatin in both gamete nuclei is described and figured as forming 8 chromosomes which are organized before the fusion. The two gamete nuclei were observed, but not figured, in contact and it was not possible to distinguish in size the male from the female. This account is then very different from those of the pteridophytes since the sperm nucleus does not enter the egg nucleus but the two fuse side by side and with their chromosomes fully organized. There are, however, some points in Kruch's paper that require more extended investigation and confirmation in the light of modern research.

There is left only the group of the thallophytes where less is known about the detailed behavior of the chromatin during fertilization than in any region of the plant kingdom. The conjugation of the gamete nuclei has been observed in a number of thallophytes, representing all of the higher groups. All of the authors, with the exception of Chmielewski ('90 b) for *Spirogyra*, describe the product of conjugation as a fusion nucleus, *i. e.*, one in which the nuclear substance of both gametes is contained within a common nuclear membrane. The most detailed accounts of the fusion of gamete nuclei in the thallophytes are those for *Fucus* (Strasburger, '97 a; Farmer and Williams, '98).

The sperm of *Fucus* upon entering the egg loses its cytoplasm and passes rapidly to the egg nucleus as a deeply staining body resembling a plastid in form. This structure is the male nucleus whose chromatin is so densely crowded that it stains too deeply to show much structure. Arriving at the side of the female nucleus, about ten minutes after its entrance into the egg, the male nucleus flattens against the female and increases in size so that the chromatin appears less condensed. The male nucleus is then absorbed so that the paternal chromatin lies within a fusion nucleus but may be distinguished for some time as densely staining material at one side. A second nucleolus often appears in the fusion nucleus in the vicinity of the paternal chromatin and is probably associated with the entrance of the sperm nucleus, although it is not likely to have been brought in as an organized structure but developed later at the expense of material in the sperm nucleus. The fusion nucleus remains quiescent for from 20 to 24 hours during which time the paternal chromatin becomes so distributed that it can no longer be followed. Then two centrospheres with conspicuous radiations appear at opposite poles of the fusion nucleus and the first cleavage spindle is organized. There is no evidence that either of these centrospheres is brought into the egg by the sperm and both appear *de novo* and independently of one another.

The chief accounts of the fusion of gamete nuclei in thallophytes are as follows: *Closterium* and *Cosmarium* (Klebahn, '91); *Rhopalodia* (Klebahn, '96); *Cocconeis* (Karsten, :00); *Sphæroplea* (Klebahn, '99; Golenkin, '99); *Ædogonium* (Klebahn, '92); *Coleochaeta* (Oltmanns, '98); *Vaucheria* (Oltmanns, '95; Davis, :04); *Fucus* (Strasburger, '97a; Farmer and Williams, '98); *Batrachospermum* (Schmidle, '99; Osterhout, :00); *Nemalion* (Wolfe, :04); *Basidiobolus* (Fairchild, '97); *Albugo* (Wager, '96; Stevens, '99, :01 b; Davis, :00); *Peronospora* (Wager, :00); *Pythium* (Miyake, :01; Trow, :01); *Achlya* (Trow, :04); *Araiospora* (King, :03); *Sphærotheca* (Harper, '95); *Pyronema* (Harper, :00). Most of these papers with others on fertilization in the thallophytes are summarized by Mottier, (:04 b) in very convenient form for reference.

There is some confusion in the accounts of fertilization in

Spirogyra which should be thoroughly investigated. Chmielewski ('90b) in a paper published in Russian and reviewed in the *Bot. Centralb.*, vol. 50, p. 264, 1892, described a fusion of the gamete nuclei in the zygospore and an immediate mitosis, without a period of rest, followed at once by a second division of the daughter nuclei. These mitoses give the zygospore four nuclei, two of which unite to form a final resting nucleus in the zygospore while the remaining two fragment and their products finally break down. This behavior offers an exception to all sexual processes so far known in the plant kingdom. There are some features which suggest a possible confusion with events as described in the zygospore of the desmid and the auxospores of certain diatoms.

The fusion nucleus in the zygospore of *Closterium* and *Cosmarium* (Klebahn, '91) divides into four at the time of germination and two of these break down while each of the others becomes the nucleus of the two new desmids that are formed. There is then in the desmids the division of the fusion nucleus into four but no secondary nuclear fusions as Chmielewski reports for *Spirogyra*. In certain diatoms, *Rhopalodia* (Klebahn, '96) and *Cocconeis* (Karsten, :00), there is a preliminary division of the nuclei in each of the two cells which form the auxospore. In *Rhopalodia* the mitoses are carried so far that four daughter nuclei are formed in each diatom and the protoplasm divides into two cells each of which fuses with a corresponding cell of the companion pair. In both types the superfluous nuclei break down so that the conjugating cells have each a single functional gamete nucleus. There are then complications in the Conjugales and the diatoms, which make nuclear studies of the sexual processes exceptionally difficult and we seem justified in reserving our judgment of the results of Chmielewski until confirmed. It seems possible that the mitoses following the germination of the zygospore in the Conjugales with the attendant nuclear degeneration are reducing divisions in a simple and primitive type of sporophyte generation but more detailed studies of nuclear behavior during the formation and germination of the zygospore will be necessary to settle the discussion.

We have now finished our account of nuclear fusions in the

sexual act (fertilization) but there remains for consideration the behavior of certain cytoplasmic elements introduced into the sexually formed cell, especially chromatophores and the blepharoplast. Since the blepharoplast bears a very close resemblance to the middle piece of the animal spermatozoon, which sometimes becomes a centrosome in the animal egg, a critical comparison of the behavior of these two structures during fertilization is full of interest.

Except for certain accounts of *Spirogyra*, to be described in the next paragraph, investigators agree that the chromatophores or plastids of gametes never fuse in the sexually formed spore. Plastids have not been found in the sperms of the gymnosperms, pteridophytes, nor bryophytes. The sperms of some algæ also appear quite colorless at maturity but careful examinations have shown in a number of forms a very small chromatophore in the early stages of development. Other less highly differentiated sperms are known to have chromatophores (*e. g.*, *Sphaeroplea*, *Cutleria*, *Volvox*). Both gametes in the isogamous types of sexuality among the algæ always have chromatophores or plastids. These have been followed in detail through stages of fertilization in *Ectocarpus* by Berthold ('81) and Oltmanns ('99), and in *Scytosiphon* by Kuckuck ('98) where it is evident that they do not unite and there is no reason for believing that different conditions obtain among any of the lower forms such as *Ulothrix*, *Cladophora*, *Hydrodictyon*, etc., although detailed observations are greatly lacking on this point, chiefly because the conjugating cells are generally very small.

Early accounts of the formation of the zygospore of *Spirogyra* have reported some form of union of the chlorophyll bands of the two gametes. The last work upon the subject, Chmielewski ('90a), reviews the results of previous investigators and gives a detailed account of a species of *Rynchonema* (*Spirogyra*). Chmielewski claims that the chromatophore of the gamete (male) that passes over into the other cell (female) becomes disorganized as the zygospore develops. While the chlorophyll band of the female cell retains much of its color, that from the male becomes yellowish and breaks up into fragments which become scattered in the zygospore and finally break down. This inter-

esting account accompanied by clear figures gives an explanation far more in keeping with what we know and might expect of the behavior of chromatophores in resting spores. That the green chromatophore may temporarily become much modified in color and form is well known in some of the red and orange resting spores of the Volvocaceæ and the zygosporos of the desmids. In some of these types the form and color of the chromatophores become quite lost for the time being so that studies on their behavior are very difficult. For these reasons it seems probable that the accounts of the fusion of the chromatophore in the zygosporos of *Spirogyra* are incorrect. It is very interesting that the gametes of *Spirogyra* should be so sharply differentiated that the chromatophore of one should be reduced during conjugation in a manner that resembles very closely the behavior of the chromatophore in highly differentiated sperms.

There is no evidence that the pigment spots, so generally present in the motile gametes of lower forms, ever unite. They have been followed into the zygosporos and after the germination of this cell and they remain entirely independent of one another as would be expected from their close relationships to chromatophores.

The fate of the blepharoplast will now be considered. This structure is especially interesting because of its close analogy to the locomotor apparatus of the animal spermatozoön, which is formed chiefly from one or more centrosomes generally with the coöperation of archoplasm (idiosome, Nebenkern). It is also claimed by a number of zoölogists that in some forms, at least, the centrosomes of the first cleavage spindle are derived from the spermatozoön.

All evidence indicates that the blepharoplast of the plant sperm is left behind in the cytoplasm of the egg when the male nucleus passes into the interior to unite with the female and that centrospheres when present, in the first cleavage spindle, are formed *de novo*. The fate of the blepharoplast is clearly known in *Cycas* (Ikeno, '98b), *Zamia* (Webber, :01) and *Ginkgo* (Ikeno, :01). Soon after the large top-shaped sperm of these forms enters the egg, the male nucleus slips out of the spiral blepharoplast, that partially invests it, and, leaving it with

other cytoplasm of the sperm at the end of the egg, passes quickly to the center to unite with the female nucleus. The blepharoplast remains near the periphery of the egg and may be recognized even after the gamete nuclei have united. It finally breaks down and its substance becomes lost in the cytoplasm of the egg. The most complete account of the history of the blepharoplast in the fertilized egg is that of Webber (:01). We should naturally expect the first cleavage spindle in the cycads and Ginkgo to be developed as in the conifers. Ikeno (:01) described clearly an intranuclear spindle in Ginkgo. In the conifers, as previously described, the first cleavage spindle is intranuclear and the fibers are developed freely from a mesh and form a broad poled spindle without centrospheres. So that not only does the blepharoplast break down at a distance from the egg nucleus but we have no reason to think that there is any place for a centrosome in the history of the first cleavage spindle in the gymnosperms.

We do not know clearly the fate of the blepharoplast in the egg of any pteridophyte or bryophyte, although Shaw's ('98a) studies on *Onoclea* indicate that it breaks down in the cytoplasm. Our knowledge of the thallophytes is equally incomplete as regards the history of the blepharoplast in the egg. But both Strasburger ('97a) and Farmer and Williams ('98) have agreed for *Fucus* that the two centrospheres at the poles of the first cleavage spindle develop *de novo* and independently of one another, and Williams (:04b) holds the same view for the centrosphere which appears at the side of the fertilized egg of *Dictyota*. The sperms of the thallophytes are generally very small cells and it may prove a difficult matter to follow their blepharoplasts so that our opinions of events in these forms are likely to be largely inferential from our knowledge in higher groups.

We can safely say that there is no evidence that the blepharoplast ever enters into the first cleavage spindle which is certainly developed in the spermatophytes and probably in the pteridophytes without centrosomes or centrospheres. Where centrosomes or centrospheres are known for the first cleavage spindle in the thallophytes (*Fucus* and *Dictyota*), the observations indi-

cate that such structures have not come from the blepharoplast. Williams' (:04b) recent work on Dictyota, while incomplete in the series of stages illustrating the fusion of gamete nuclei (fertilization), presents a very interesting comparison of the development of the first cleavage spindle in fertilized eggs with parthenogenetic eggs. In the fertilized egg there is regularly found a centrosphere which apparently divides into two that separate until they lie at opposite poles of the mature spindle. In the parthenogenetic egg, on the contrary, the spindle is multipolar and develops very irregularly from a kinoplasmic mesh which is intranuclear and there is no sign of centrospheres. Williams believes that fertilization enables the fusion nucleus to form *de novo* a centrosphere external to itself which is not possible for the nucleus of a parthenogenetic egg.

It should be noted that these conclusions are all against the view that the centrosome is a permanent organ of the cell and that the blepharoplast holds any direct relation to centrosomes when present in the first cleavage spindle and inferentially rather strengthens the doubt that the blepharoplast is derived from a centrosome, which point was discussed in our account of the sperm in Section III. However, Ikeno (:04) in a paper which arrived too late to be treated in Section III, is very positive that blepharoplasts are centrosomes, presenting his evidence clearly, but his explanation of the conditions under which blepharoplasts are formed from the plasma membrane does not seem to me conclusive, especially in the light of Mottier's (:04a) recent paper on Chara, which also could not be treated in Section III (see *Amer. Nat.*, vol. 38, p. 576, 1904).

3. Asexual Cell Unions and Nuclear Fusions.

As stated earlier in the paper, the test of a sexual act must lie with the history of the elements which unite, unless we choose to treat sexuality as a purely physiological process and disregard its relation to morphology in ontogeny and phylogeny. This relation is so precise, *i. e.*, sexuality is so firmly established as a fixed period in the life history of most organisms, that the biologist generally thinks of the sexual process as a part of the

life history, which must take place with as much regularity as the normal development of any organ. As a matter of fact, our knowledge of the structure of sexual elements and the events of sexual phenomena is almost wholly morphological and for the present at least it seems safer to treat and define sexuality from a morphological standpoint.

Under asexual cell unions and nuclear fusions we shall include a number of interesting phenomena which can be arranged in three groups: (1) cell fusions which have apparently no sexual relations; (2) cell fusions which are substitutes for a normal ancestral sexual process now suppressed; and (3) extraordinary modifications of what may have been originally sexual processes but which at present serve some peculiar and special function.

In the first group will be included the extensive union of swarm spores, or the amœboid elements derived from such, best illustrated in the development of plasmodia; also such cell fusions as are clearly for nutritive purposes, as is the union of the sporophytic portion of the cystocarp of the red algæ with auxiliary cells and probably also the fusion of sporidia in the smuts and the conjugation of yeast cells. The second group embraces the interesting fusions of the nuclei in teleutospores of the smuts and rusts and in the basidium with the previous history of the paired (conjugate) nuclei in the mycelium, perhaps also the nuclear fusions in the ascus, and such cell unions as have been reported preliminary to the apogamous development of the fern sporophyte. The third group includes the remarkable phenomenon in the embryo sac, the double fusions of the polar nuclei and the triple fusion of these with the second sperm nucleus, frequently called "double fertilization."

The well known union of the swarm spores of the Myxomycetes as amœboid cells (myxamœbæ) to form the plasmodium is one of the best illustrations of a fusion of protoplasm without sexual significance. In this general union of hundreds and perhaps thousands of small cells there are no nuclear fusions so far as is known, but simply the merging of the cytoplasm to form a large multinucleate unit. The whole phenomenon indicates a coöperative process which is probably economical of nutritive functions in the semiterrestrial conditions under which plas-

modia live. It is quite possible that the origin of sex may have been involved with some of the same principles as those which bring about the union of swarmers to form a plasmodium, but the added features of nuclear fusion together with the history of the sexually formed cells which become in higher groups the starting point of a sporophyte generation places the sexual act on a very much higher level of complexity.

There are some records of the union of several zoöspores or gametes to form a zygosporé instead of the usual conjugation in pairs. The biciliate gametes of *Acetabularia* (De Bary and Strasburger, '77) sometimes conjugate in threes and large zygotes are figured with five pairs of cilia indicating that as many gametes entered into their formation. The gametes of *Protosiphon*, described by Rostafinski and Woronin ('77) as in the life cycle of *Botrydium*, are reported by them to unite at times several together and four are so figured. Klebs ('96, p. 207) in his account of *Protosiphon* also noted the union of the gametes in threes especially when in organic solutions. The significance of these multiple fusions of swarm spores is not clear for we know nothing of the nuclear history following the union. There is in the habit, however, such a resemblance to the extensive union of swarmers in the *Myxomycetes* as to indicate that primarily sexuality may have been concerned chiefly with cytoplasmic fusions and associated very intimately with nutritive processes. I have recently observed several instances of the conjugation of zoöspores of *Saprolegnia* when the elements united in pairs at the ciliated ends and along the sides exactly as do motile gametes, and the fused cell bore four cilia. The zoöspores of *Saprolegnia* are too far removed morphologically from the highly differentiated sexual organs of the group to justify the explanation of such conjugation as a sexual act and we must think of it as due to some peculiarities of nutritive conditions.

Another class of very interesting cell fusions, associated with nutritive functions, is presented in the union of the sporophytic fertile filaments (oöblastema filaments) in the cystocarp of the *Rhodophyceæ* with auxiliary cells. This phenomenon which was regarded by Schmitz and his followers as sexual in charac-

ter, is considered by Oltmanns ('98b) to have nutritive relations alone. Oltmanns studied the fusion with auxiliary cells in several genera, but especially for *Callithamnion* and *Dudresnaya*, and is satisfied that the cell unions concern only the cytoplasm. Fertilization takes place with the fusion of gamete nuclei in the carpogonia and these cells develop the sporophyte generations. The fusion of fertilized carpogonia or filaments derived from them with auxiliary cells, is a feature of a sort of semiparasitic relation that the sporophyte holds to the gametophyte by which it is nourished in part through organic connections with the gametophyte. The nuclei of the sporophytic structures remain quite apart from those of the auxiliary cells so that the union is purely cytoplasmic. This theory of Oltmanns has received strong support through the detailed nuclear studies of Wolfe (:04) on fertilization and the development of the cystocarp of *Nemalion* who finds cytological evidence of the sporophytic character of the cystocarp. These papers of Oltmanns and Wolfe have been discussed by myself in the *Bot. Gaz.*, vol. 27, p. 314, 1899, and vol. 39, p. 64, 1905.

Writers have at times attached sexual significance to the conspicuous fusions between sporidia of certain of the *Ustilaginales* (*e. g.*, *Tilletia*). But there seems at present no reason to regard this phenomenon as different from the cytoplasmic connections frequently established between cells of hyphæ which are ultimately associated in a common mycelium where the whole forms a close unit with respect to common nutritive relations. Such protoplasmic connections were treated in the first part of this section. Harper ('99a) studied the union of conidia and cells of the promycelium in *Ustilago* and concluded that the fusions involve the cytoplasm alone, there being no nuclear changes. However, Federley (:03-:04; review in *Bot. Zeit.*, vol. 62, p. 171, 1904) has observed the migration of a nucleus from one conidium to another in *Ustilago tragopogonis pratensis* (Pers.), and a fusion within the latter. This nuclear fusion was not found in some other forms of *Ustilago* which behaved as Harper has described. There is nothing in the morphology of the conidia to indicate that they are sexual cells and from what we know of the life history of Basidiomycetes we should look

for sexual processes at other periods more closely associated with the development of teleutospores or basidia.

The conjugation of yeast cells has many points of similarity to the fusion of conidia in the Ustilaginales. This phenomenon has been discovered in an organism obtained from commercial ginger by Barker (:01), which he calls *Zygosaccharomyces*, and in three species of *Schizosaccharomyces* by Guilliermond (:03). The conjugation in all forms immediately precedes spore formation and involves a nuclear fusion as well as that of the cytoplasm. The conjugation is followed by division of the fusion nucleus and spore formation in the united cells. The conjugating cells are sisters in the species of *Schizosaccharomyces* but apparently may not be closely related in Barker's form, *Zygosaccharomyces*. Both investigators regard the conjugation as a sexual act, and Guilliermond considers the fusion cell to be an ascus with the value of a zygosporangium. These conclusions do not seem to the writer convincing. Spore formation in the yeasts has not been shown to present any of the peculiarities of nuclear division and free cell formation as described by Harper for the ascus, and until such are established it is hardly safe to conclude that the yeasts are Ascomycetes. Whether or not the conjugation is a sexual process becomes a question of phylogeny and we know too little of the history and relationships of the yeasts to assert that the conjugating cells are morphologically gametes. Again, the view that yeasts are derived from conidia or mycelia of higher fungi which have continued a simple growth by budding in peculiar and favorable media is rather against any view that we are dealing here with a simple or primitive sexual act. There are very striking resemblances to the fusions of conidia in the Ustilaginales, which were described in the previous paragraph and do not appear to be sexual processes. It is unsafe to assume sexuality because the conjugation precedes spore formation, because in most yeasts spore formation takes place regularly without conjugation. Is it not rather another illustration of cell and nuclear fusions related to nutritive processes alone?

Some of the most interesting nuclear fusions, apparently associated with the apogamous development of a sporophyte are

the unions of the pairs of nuclei which enter the cells of the developing teleutospores of the Uredinales and Ustilaginales and the basidium of higher Basidiomycetes. It has been established through the studies of a number of investigators (chiefly Rosen, '93; Dangeard and Sapin-Trouffy, '93; Dangeard '93, '94-'95a, c; Poirault and Raciborski, '95; Sapin-Trouffy, '96; Maire, :00 a, b, c, :02; Holden and Harper, :03) that the æcidiospores and the mycelium derived from them and preceding the development of the uredospores and teleutospores contain pairs of nuclei which divide in such a manner (conjugate division) that the nuclei of the pair are derived through two unbroken lines of succession for a long vegetative period and always maintain complete independence of one another. Every young teleutospore and basidium contains such a pair of nuclei which shortly fuse so that the mature structure is uninucleate. Dangeard and Sapin-Trouffy have from the first regarded the nuclear fusion within the teleutospore, whether of rust or smut, as a sexual act and the ripe teleutospore a fertilized egg, regardless of the fact that its morphology was not that of any known sexual organs. Dangeard ('94-'95 c; :00) likewise considered the nuclear fusions in the basidium as sexual. Raciborski ('96) suggested that the series of conjugate mitoses leading to the nuclear fusions in the teleutospore represented a vegetative phase intercalated between the beginning of a sexual act and its finish in the teleutospore. His explanation, in the light of the recent paper of Blackman (:04a), was nearest the truth. Maire (:02) presents the most extensive account of the nuclear structure in the higher Basidiomycetes previous to and during the formation of the basidia. He held that the fusion of the paired nuclei (synkaryon) in the basidium was not the whole act of fertilization which must begin with the formation of the paired nuclei. Maire (:02, p. 189) gave some suggestions as to how and where the paired nuclei arose but neither he nor any of the authors mentioned above knew clearly their origin.

Blackman (:04a) has made the most important contribution to the subject of fertilization and alternation of generation in the Uredinales, showing clearly that the paired nuclei appear in the life history of *Phragmidium violaceum* and *Gymnosporangium*

clavariæforme just before the development of the æcidium. They arise in Phragmidium by the migration of a nucleus from an adjacent cell into an element (the fertile cell) which represents a female sexual organ. The morphology of the female organ is not clear but there are suggestions of a structure similar to the procarys of the Rhodophyceæ and Laboulbeniales. The fertile cell, after receiving its second nucleus, develops a chain of æcidiospores, the two nuclei becoming so closely associated in the paired condition that they divide simultaneously (conjugate mitosis) from now on until the teleutospores are formed. Thus the cells of all mycelium beginning with the æcidiospore contain paired nuclei up to the development of the teleutospores, including of course the uredospores when present. This period of the life history may be considered as representing a sporophyte generation, especially since the total of chromatin in the pair of nuclei is double the amount when the nuclei are solitary. The sporophyte phase ends with the fusion of the pair of nuclei in each cell of the teleutospores and in the reduction phenomena that take place with the germination of the teleutospore, including the formation of the promycelium. The sporidia developed by the promycelium are uninucleate and the cells of the mycelium derived from them are uninucleate up to the production of the æcidium. This constitutes the gametophyte phase of the life history. The spermogonia by their morphology seem to be male organs, now functionless.

In such of the Uredinales as have no æcidium, as also in the higher Basidiomycetes and the Ustilaginales, it is probable that both sexual organs are suppressed since no trace of such structures has been found. However, we may expect to discover periods in all of these forms when paired nuclei come into the life history and after a series of conjugate divisions fuse in the teleutospore or basidium. Such pairs of nuclei, as stated before, are known in the Ustilaginales (Dangeard, '93) and in a number of forms of the Uredinales and the nuclear fusions have been followed in the teleutospore. Holden and Harper (:03) have given an especially clear account of the paired nuclei in the mycelium and uredospores of *Coleosporium* together with their fusion in the teleutospore. Maire (:02) describes the paired

nuclei (synkaryons) and their fusion in the basidium in a large number of Hymenomycetes and Gasteromycetes.

Evidence is thus accumulating that the cells in the mycelium of higher Basidiomycetes (Hymenomycetes and Gasteromycetes) are binucleate for extended periods previous to the formation of basidia where nuclear fusions always take place. Binucleate cells in the higher Basidiomycetes were first reported by Maire (: ooa ; : oob), in the tissue preliminary to spore formation. He also confirmed Dangeard ('94-'95c) in his view that only two nuclei unite in the basidium contrary to accounts of Rosen ('93) and Wager ('99, p. 586) which described a succession of fusions involving sometimes as many as six or eight nuclei. Harper (:02) has given for *Hypochnus* one of the most complete accounts of the behavior of paired nuclei previous to and during the development of the basidium. The cells of the mycelium of this simple Hymenomycete were found to be binucleate as far back as they were studied which included all of the conspicuous vegetative structure. Only a single pair of nuclei enters the basidium and fuses. Harper's results are then in agreement with the extended observations of Maire (:02) as are also the detailed studies of Ruhland (:01) on a number of forms and Bambeke (:03). Taken together they seem to show clearly that the mycelium, for long periods preliminary to the formation of basidia, contains paired nuclei and that the basidia receive each a single pair, which nuclei fuse. There is thus an exact correspondence between the life histories of the Ustilaginales, Uredinales, and higher Basidiomycetes with respect to the period of paired nuclei and their fusion in the teleutospore or basidium. Dangeard called the fusion in the basidium a sexual act and the structure an oöspore regardless of the morphological difficulties of such a conception. Maire (:02, p. 202) states that the origin of the paired nuclei is the only phenomenon strictly comparable to fertilization and Blackman's studies support this view. Ruhland (:01) regards the conditions as a deviation from the normal type of sexuality calling it "intracellular karyogamy." The origin of the paired nuclei is not known for any higher Basidiomycete and the discovery of this period and determination of the events leading to the change from uninucleate mycelium to

binucleate is one of the most interesting problems in this field of botany. This is the point where we should expect to find the remains of sexual organs, if any are present in the higher Basidiomycetes, but it is not likely that they will be found. It seems more probable that the mycelium with the paired nuclei (perhaps sporophytic in character) arises apogamously with a complete suppression of the sexual organs in agreement with such of the Uredinales as have no æcidium and the Ustilaginales.

Blackman's explanation of the history of the paired nuclei in *Phragmidium* is full of interest. As stated before, he regards the fertile cell which develops a chain of æcidiospores, "as a female reproductive cell which undergoes a process of fertilization" by a union with an adjacent cell of the mycelium and its reception therefrom of a nucleus. The mycelium then which arises with the æcidiospore is sporophytic in character and so remains until the fusion of the pairs of nuclei in the teleutospores. The male organs of the rusts are the spermatogonia and the male gametes the spermatia which are of course now functionless so that the "process of fertilization" is through the introduction into the female cell of a nucleus which is not phylogenetically a male sexual element. Blackman's (:04 a, pp. 349-353; :04 b) conception of the process as an act of fertilization involves some principles which will be briefly outlined.

Blackman believes for *Phragmidium* "that the primitive normal process of fertilization by means of spermatia has been replaced by fertilization of the female cell through the nucleus of an ordinary vegetative cell" and regards the process as very similar to the phenomenon reported in the apogamous development of ferns by Farmer, Moore, and Digby (:03), which will be considered presently. Blackman points out that normal processes of fertilization such as we have included under the head of "sexual cell unions and nuclear fusions" do not involve in many forms (probably all types with a sporophyte generation) an immediate union of the chromatin of the sexual nuclei which is known to remain distinct during the first cleavage mitosis in a number of types (*e. g.*, *Pinus* and some other gymnosperms). So there is nothing in the delayed fusion of the paired nuclei up to the teleutospore that is seriously against his explanation of the "fer-

tilization" of the female cell of the Uredinales. Indeed, we may expect to find that the actual fusion of paternal and maternal chromatin does not take place in the higher plants until the end of the sporophyte generation in the spore mother cell, as zoölogists have concluded that such union occurs just previous to gametogenesis in animals. But is Blackman justified in regarding the phenomenon substituted for the activities of ancestral sexual organs in *Phragmidium*, now functionless, as a sexual act and is it desirable to apply the term fertilization to the phenomenon?

Blackman (:04 b, p. 153) speaks of the introduction of a nucleus into the fertile cell of the Uredinales and the phenomenon in the apogamous development of the fern after the account of Farmer, Moore, and Digby (:03) as "reduced forms of fertilization." It may be questioned whether the use of the term fertilization is fully justified by the events under discussion. We are all likely to agree with these authors that the physiological aspects of the phenomena in the cases under consideration are similar to sexual acts. But, by the writer, the act of fertilization is always considered in phylogenetic relations and strictly limited to the union of sexually differentiated cells, which are defined by their morphology through principles of homology. Whenever one or both of the gametes are suppressed in a life history and a succeeding generation develops of the sort that normally follows a sexual act, then such a development is apogamous and the phenomena always introduce features which are foreign to the processes of normal fertilization and the fundamental principles of sexuality.

Perhaps the most important characteristic of sexuality from an evolutionary standpoint is the fusion of gametes of unrelated parentage, for in the mingling of diverse protoplasm lie two factors: (1) a physiological stimulus to development, and (2) an increased probability of inherited variation which in new combinations will appear to the advantage of the species. Blackman's "reduced forms of fertilization" which I should prefer to consider apart from normal fertilization as examples of apogamy, and have so classed in this treatment, do satisfy the physiological requirements of a sexual act in that a form of nuclear fusion

is substituted for the union of gamete nuclei but the phylogenetic and evolutionary aspects of sexuality are disregarded. Also, the nuclei that fuse are sometimes very closely related, which is a condition generally avoided in sexual processes except where peculiarities of habit make close inbreeding necessary. It is true that large groups, such as the Basidiomycetes, perhaps certain regions of the Ascomycetes, some Phycomycetes, and some forms of the higher plants and algæ seem to have given up normal sexual processes but there is much evidence that in many cases this loss of sexuality is associated with a certain degree of segregation and with peculiarities of life conditions apart from the normal activities of all organisms or quite different from the ancestral stock. The groups are likely to be distinguished by highly specialized life habits of a sort that make it impossible for inherited sexual organs to function, either through mechanical difficulties or because one or both degenerate. It seems to me much clearer to regard all illustrations of Blackman's "reduced forms of fertilization" under the general term of apogamy even though it may be clear that they are physiological substitutes for sexual acts and to reserve the term fertilization for the union of gametes which can always be clearly identified through morphology in ontogeny and phylogeny. The success of a group even though ancestral sexual processes may be suppressed does not enter into a problem which is at bottom a morphological one. Success is relative and we really have no means of estimating its degree save by actual experiment. It is not likely that any biologist would claim that sexual degeneration is advantageous to any species although the organic world is full of forms which have dispensed with sexuality and still hold their places. These are the reasons why I have grouped cell unions and nuclear fusions as sexual and asexual on a morphological basis founded on phylogenetic principles and why in Section V, we shall devote some attention to the substitutes for sexuality under the head of apogamy.

The Ascomycetes present a phenomenon of nuclear fusion within the ascus which may properly be considered at this time since there is a certain resemblance to the nuclear fusions in the teleutospore and basidium. Dangeard ('94-'95b) gave the

first account of this phenomenon describing it for several forms. The mother cell of an ascus sometimes terminates a hypha but more commonly is situated a little back from the end at a point where the hypha bends abruptly like a knee. The mother cell contains two nuclei, closely related to each other, that unite, after which the fusion nucleus divides to form the ascospores. Dangeard considered this fusion to be a sexual act and the product an oöspore which germinates immediately to form the ascus. He regards the ascus as a sporangium, and equivalent to the promycelium which he calls a conidiophore. Dangeard is not willing to accept any of the evidence that the ascocarp ever results from a sexual act or that sexual organs either functional or abortive are present at any stage in the life history of Ascomycetes. Sexuality, according to him, is reduced to the fusion within the ascus alone. He (Dangeard, '96-'97a, b; :00) discredits the work of Harper on *Sphærotheca*, *Erysiphe*, and *Pyronema* and the older accounts of De Bary and his pupils on sexual organs of the Ascomycetes. A series of short papers in *Le Botaniste* (:03, Fas. 1) presents Dangeard's last attack on the work of Harper and a reaffirmation of his peculiar views.

Harper's description of sexual processes in *Sphærotheca* ('95; '96) *Erysiphe* ('96), and *Pyronema* (:00b) are so convincing that, together with our knowledge of sexual organs in the lichens, Laboulbeniales, and Gymnoascales, we must accept the old view of De Bary that the ascocarp represents a development (probably sporophytic) from a sexual phase even though it may be established that there is much apogamy in the Ascomycetes. Harper gives the clearest account of the nuclear fusion in the ascus of any author without, however, committing himself to speculations on its significance. The subject is well summarized in his paper on *Pyronema* (:00b, pp. 363, 394). He finds in *Erysiphe*, *Pyronema*, and some other forms that the ascus is always developed from a penultimate cell of a hypha which bends sharply so that this cell appears to lie at the tip. There are two nuclei at the end of the ascogenous hypha and these divide simultaneously in a very characteristic manner so that the young ascus receives two of the resultant four nuclei, but each is derived from a different one of the original pair and

consequently they are not sisters. The two nuclei in the ascus then fuse. The origin of the original pair is not known.

No satisfactory explanation of this fusion in the ascus has been advanced. The conditions in the Ascomycetes are not the same as in the Basidiomycetes. There is no series of paired nuclei in the ascogenous hyphæ and no evidence of a delayed fusion of gamete nuclei following a sexual act nor of nuclear fusions associated with the apogamous development of a sporophyte generation. On the contrary, a sexual act with the fusion of gamete nuclei has been clearly established in some forms preliminary to the development of the ascocarp and the nuclear union in the ascus is plainly a supplementary phenomenon. Wager and Harper point out analogies to the account of Chmielewski ('90b) for *Spirogyra*, considered in a previous part of this section, which described a double nuclear fusion in the zygospor. Thus the primary, sexually formed nucleus of the zygospor is reported to divide into four secondary nuclei, two of which break down while the remaining two unite forming the second and final fusion nucleus of the spore. It is hard to see how these second nuclear fusions can be sexual and Groom ('98) is perhaps correct in considering them superimposed on the sexual act, but their physiological significance is not clear.

Some recent papers support in general Harper's investigations on the ascus. Guilliermond (:04a; :04b) describes the development of the ascus and ascospores in a number of forms. In an unnamed species of *Peziza* he found, however, that the ascus developed from the terminal cell of the ascogenous hypha which received two nuclei (that fuse) of the four that are found at the tip. Maire (:03a; :03b) has reported a similar history for *Galactinia succosa*. Both Maire and Guilliermond note the resemblance of these conditions to the nuclear associations in the young basidium and Maire does not hesitate to consider the two nuclei in the tip of the ascogenous hypha as much reduced synkaryons, (paired nuclei) appearing for a very short period just previous to the nuclear fusions in the ascus. Maire follows Dangeard in denying the sexual processes described by Harper in the Ascomycetes and would allign the events in the ascus with those in the basidium. Guilliermond agrees with

Harper that the number of chromosomes presented in the mitoses within the ascus is large (8, 12, 16, in various species) as against Dangeard and Maire who have claimed that the number is uniformly 4. Guilliermond's account of spore formation in the ascus supports that of Harper (described in Section II) in all essentials and gives especial attention to the structure of the epiplasm and its inclusions.

In summary: the significance of the nuclear fusions in the ascus seems very much of a mystery. If they could be associated with an apogamous development of the ascocarp we should have conditions analogous to those in the Basidiomycetes but following a sexual act as it does in *Sphærotheca*, *Erysiphe*, and *Pyronema* we find a phenomenon whose *raison d'être* is not apparent. However, we do not know the history of the nuclei preceding the group of four at the end of the ascogenous hypha and perhaps it may be discovered that events at this period are concerned with nuclear reduction at the end of a sporophyte generation.

One of the most interesting announcements of recent months is that in a preliminary note of Farmer, Moore, and Digby (:03) on the nuclear history preceding the apogamous development of a species of *Nephrodium*. They found that the cells of the prothallus at the point where the sporophyte arose became binucleate by the migration of nuclei from neighboring cells. The two nuclei might remain separate for some time or fuse at once. The authors speak of the whole process "as a kind of irregular fertilization" and Blackman considers it analogous to the entrance of the nucleus into the fertile cell of *Phragmidium* and the establishment of the paired nuclei in the *Uredinales*. As we discussed the phenomenon in that connection I considered the use of the term fertilization unfortunate since it included processes which however similar physiologically held no relation morphologically and phylogenetically to normal sexual processes. As stated then, it seems to me much clearer to regard all such apogamous phenomena apart from sexual processes, pointing out as far as possible physiological resemblances but recognizing the wide gap in morphology established by the past evolutionary history of the plant. The interest in the phe-

nomena does not become less by this treatment which certainly avoids much confusion of expression.

There is left for consideration one other group of nuclear fusions which may have sexual significance although such is not obvious, namely the fusions of polar nuclei in the embryo sac of angiosperms and the triple unions of the above with a second sperm nucleus which is often called "double fertilization." Several excellent reviews of this subject have appeared, notably by Strasburger (:00b), Sargent (:00), Coulter and Chamberlain (:03), Mottier (:04a, b), and Guérin (:04). The explanation of this phenomenon is likely to rest finally upon morphological analysis but at present we are uncertain of the homologies of the polar nuclei and the part they play in the evolutionary history of the endosperm. The most striking theory of the endosperm was proposed by LeMonnier ('87) who suggested that the fusion of the polar nuclei gave origin to a second embryo modified to nourish the normal embryo. One of the polar nuclei is always closely related to the egg nucleus so that in the triple fusions (the sperm with two polar nuclei) we have conditions very close to normal fertilization, the discordant element being not the sperm nucleus but the antipodal polar nucleus. The triple fusions would seem at first thought to be rather favorable to LeMonnier's theory although it is plain that with such a diverse mixture of chromatin from three nuclei the resultant structure can scarcely be called a sporophyte embryo from the very grotesqueness of its make-up. Miss Sargent considers the fusion of the second sperm with the micropylar nucleus as sexual in character but so complicated by the introduction of the antipodal polar nucleus that the result is a bizarre structure not strictly comparable to a normal embryo. In the final solution of this problem we must know whether in phylogeny the sperm and micropylar polar nucleus fused first and the antipodal entered into the process later or whether the polar nuclei began the habit and the second sperm nucleus was drawn afterwards into the activities. Should the first possibility be established the sexual nature of the process would seem clear while in the second the events would be of the nature of asexual nuclear fusions. While we know very little

of the origin and evolution of the endosperm in angiosperms there is some evidence in favor of the second possibility.

Strasburger (:oob) holds that the double and triple nuclear fusions in the embryo sac are not true sexual acts even though they may involve an important principle of fertilization, namely, a stimulus to growth. According to him, sexual processes present two distinct features which he designates as "generative fertilization" and "vegetative fertilization." Generative fertilization deals with the mingling of ancestral hereditary substances in the nuclei and establishes the basis for such characters as hold the species true to its past or introduce new qualities as variations into the germ plasm. Vegetative fertilization brings to the fusion nucleus simply a stimulus to growth such as may be given to unfertilized eggs by changes in their physical and chemical environment. We might apply this classification to many of the examples of asexual nuclear fusions which we have discussed, as in the apogamous development of the fern and the origin of the paired nuclei in the rusts, and they have the elements of vegetative fertilization in Strasburger's sense. But such distinctions are very subtle and it seems rather doubtful whether they add much to the clearness of our conceptions. The growth stimulus of "vegetative fertilization" is always an accompaniment of "generative fertilization" and would be expected of any cell unions or nuclear fusions. The peculiarities of sex lie in the phylogenetic features of the phenomena, *i. e.*, in the union of differentiated gametes with their long evolutionary history and not in the mere fusion of any nuclei at any time.

From this point of view the double fusions of polar nuclei or the triple fusions, when a sperm nucleus becomes involved in the phenomenon, are of very doubtful sexual nature since no phylogenetic connections have been established with the normal sexual processes of the spermatophytes. Indeed, there are many irregularities in the process of endosperm formation which complicate the discussion and make it very difficult to trace relationships. Thus nuclear fusions are described in the late stages of endosperm formation when several of the free nuclei become included in the same cell area by the formation of the cell walls

(*Corydalis*, Strasburger, '80; Tischler, :00; *Canna*, Humphrey, '96). Such nuclei are known to unite two or more and sometimes several together within the cells, forming fusion nuclei with a large and variable number of chromosomes. In *Peperomia* and *Gunnera* the endosperm nucleus results from the fusion of several free nuclei and a number of instances are recorded in which no fusion of the polar nuclei takes place, but the endosperm is derived from the division of one or both. Such irregularities, which will probably be greatly increased in number as investigations proceed, indicate that the double and triple fusions preceding the differentiation of the endosperm nucleus are not of phylogenetic importance but are more likely to be special developments in relation to peculiarities of seed formation among the angiosperms rather than of a sexual nature.

However, the triple fusions, when a sperm enters into the composition of the endosperm nucleus, seem to furnish a cytological explanation of the phenomenon of xenia and thus come into very close physiological relations to sexual processes. In xenia we find the effects of hybridization expressed immediately outside of the embryo in the endosperm of the seeds. If paternal chromatin has entered into the composition of the endosperm nucleus or should the sperm nucleus by itself give rise to a series of endosperm nuclei the appearance of paternal characters would be expected. This explanation of xenia was worked out independently by DeVries, Correns, and Webber, the last author having published a particularly clear and full account of the phenomenon (Webber, :00). Even though the relation of xenia to hybridization is apparent, it is nevertheless clear that we are dealing with an exceptional process only possible because of the unusual conditions within the embryo sac which allow a second sperm nucleus to enter into the activities of seed formation and it is certainly not established that these activities have any phylogenetic relations to past sexual processes.

Some interesting studies of Nemec (:02-:03; :04) upon asexual nuclear fusions may open the way for explanations of some of the examples which we have considered as asexual in the latter portion of this paper. Nemec found that mitosis in the root tip of *Pisum sativum* could be checked during anaphase

by treating the material with chloral hydrate so that no walls were formed between the daughter nuclei, which remained in the common mother cell and presently fused with one another. The fusion nucleus presented a double number of chromosomes (twice that of the normal sporophyte) in succeeding mitoses which became reduced in a few hours so that later divisions showed the number characteristic of the sporophyte. Nemec regards nuclear fusions and reduction phenomena as self regulating processes which follow the vital cell fusions characteristic of fertilization. The latter (cell fusions) are then the essential phenomena of sex and nuclear activities follow automatically. Reduction phenomena are atavistic in character. Nemec considers these results in serious conflict with Strasburger's ('94) theory of the periodic reduction of the chromosomes, believing that the number of chromosomes is not so likely to give the characters of the respective sporophyte and gametophyte generations as other factors.

Nemec's contribution is chiefly of interest to us in the present connection as showing that nuclear fusions may result from disturbances of the normal environment very far removed from the conditions that produce sexual cells. And this emphasizes our contention that sexual processes must be judged through phylogenetic analysis and not by physiological resemblances. Thus the nuclear fusions in the ascus, in the basidium, preceding apogamous development of the fern, and perhaps the union of polar nuclei in the embryo sac may be involved with special physiological conditions although they resemble outwardly sexual processes and are sometimes a substitute for these. But nevertheless they are asexual nuclear fusions lacking that fundamental character of sexuality, the result of sexual evolution, namely, a fixed position in a life cycle established by phylogeny and expressed by the classic phrase "ontogeny repeats phylogeny." They are departures from the normal life history either apogamous in character or concerned with some other peculiarity of the plants' existence.

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CORRESPONDENCE.

Editor of the American Naturalist.

Sir:—Several articles have appeared in the *American Naturalist* of late on the common names of animals, and one of them introduces the question of their etymology. "There is in the human mind," as Max Müller sagely observes, "a craving after etymology, a wish to find out why such a thing should be called by such a name"; and this applies emphatically in the case of popular names in natural history.

Perhaps the most striking feature in the historical development of plant and animal vocabularies is the extent to which words have become metamorphosed, mutilated, deformed, or corrupted at the hands of the people, not only in English, but in all languages. One cannot but be impressed with the many curious travesties of the names of plants, insects, crustaceans, fishes, and higher animals which constitute a sort of verbal pathology, or "folk-etymology." There has been published recently a little essay on popular etymologies, which devotes considerable attention to instances of the latter description, and is sufficiently accurate to recommend itself to naturalists. We refer to *The Folk and their Word-Lore*, by A. Smythe Palmer (London, 1904), this being a companion work to the same author's *Folk-Etymology*.

Everyone is familiar with such typical examples of folk-etymology as "sparrow-grass," "cowcumber," and "shoe-mach," which are the popular recasting of familiar plant-names; but the majority of persons are probably unaware of the close verbal affinities existing between such words as lobster and locust, beaver and viper, crocodile and cockatrice, alligator and lizard, eagle-wood and alce, and numerous other co-derivatives whose communal origin is more or less masked. When we read in old works, for instance, that "long oysters are a sort of crayfish," we do not immediately perceive that the latter word is only a modern modification of the older *crevish* (also written *crevis* and *crevice*), which in turn is derived from the same form that has yielded the French *écrevisse*, old-high German *Chrebiz*, and modern German *Krebs*; nor does the word "long oyster" or "longoister" resolve itself at first sight into an anglicized

form of the French *langouste*, or Spanish *langosta*, which lead us back to the Latin *locusta*. The example shows, however, how it is possible for folk-etymology to transform crayfish, which are indeed a variety of shell-fish, and may properly be described as long, into a "long oyster." So too "penny-winkle" for the shell-fish commonly called periwinkle, is a partial reversion to its original form *pinewinkle*.

Many extraordinary verbal complications are brought about through the tendency to assimilate words of a foreign or unfamiliar aspect into something of like sound that shall be more intelligible. Amongst the innumerable corruptions of plant-names to which this process gives rise, may be mentioned "bloody Mars," a kind of wheat, for *blé de Mars*; "Christian anthems" for chrysanthemums; the various forms of *Polly Andrews*, *Polly Ann*, or *polander* for polyanthus; "rosy-dand drums" for rhododendrons; and the correlative "high-belie" and "low-belie" as offshoots from lobelia. Amusing illustrations of the same tendency are furnished by the soubriquets under which famous race-horses are known to grooms and jockeys. Thus, Chemisette was nicknamed *Jimmy's hat*; Othello and Desdemona were familiarized into "Old Fellow" and "Thursday Morning"; and the Irish horse Usquebaugh became to the farrier *Huskeyball*.

Professor B. K. Emerson, in relating the following anecdote, offers some instructive comments on the tendency toward assimilation, or as he calls it, "the principle of attraction in language whereby words without meaning to their users tend to be modified into forms which at least appear intelligible." Writes the genial professor¹: "Many years ago I visited the British flagship *Bellerophon* in the harbor of Bermuda, and was told that when the ship was first named, the sailors wrestled with the sonorous but unmeaning name, and quickly transformed it into 'Billy-ruffian'; and it became at once intelligible, and belligerent, and satisfying. There arose, however, a contest in the fore-castle as to whether 'Billy-ruffian' or 'Bully-ruffian' was the correct thing,—certain rude fellows of the baser sort wishing to have the word pugnacious in both its proximal and distal extremities."

The significance of this and of similar incidents that are common to everyday experience consists in their being typical of a distinct

¹ Geological Myths: Vice-Presidential Address. *Proc. Amer. Assoc. Adv. Sci.*, 1897, pp. 101-126.

process. Words are first attracted into a form which has a meaning, and in its turn this meaning requires a justification; and this the meaning itself quickly suggests. An understanding of this process has not only solved many philological problems, but finds an application in natural science. Emerson, for instance, in the address referred to, is guided by it to a rational interpretation of famous geological myths; and in the hands of Fouqué, the site of at least one volcanic eruption known to have taken place within historical times has been identified solely by linguistic clues of this nature.

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